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THE UNIVERSITY OF ALBERTA

# FOOD AND SPACE UTILIZATION BY THE PISCIVOROUS FISHES OF COLD LAKE WITH EMPHASIS ON INTRODUCED COHO SALMON

by

Wayne Emerson Roberts ©

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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EDMONTON, ALBERTA
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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Food and space utilization by the piscivorous fishes of Cold Lake with emphasis on introduced coho salmon", submitted by Wayne Emerson Roberts in partial fulfilment of the requirements for the degree of Master of Science.

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# ABSTRACT

The distribution of native fishes and introduced coho salmon was studied during the summers of 1971 and 1972. The utilization of forage fish by each species was determined.

Coho salmon appear to occupy the surface waters in the shallow ( 13.7 m) water around the lake margin, as do northern pike. Lake trout, walleye and burbot are dispersed throughout the lake but become uncommon in the shallows during August.

Coho salmon fed on ninespine sticklebacks, aerial food and to a lesser extent on other fishes and aquatic invertebrates. They differed from the native species by the inclusion of large amounts of aerial food in their diet, along with the young of the year lake whitefish and ninespine sticklebacks. Growth was rapid during the summer but poor during the winter.

Ninespine sticklebacks are the most frequently utilized forage fish in Cold Lake and are eaten by all of the known piscivorous fishes there. The native piscivorous fish prey upon the adults of this species and consume a disproportionately large number of ripe females.

# ACKNOWLEDGEMENTS

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Mr. Knut Moller, St. Paul Regional Fisheries Technician initiated the netting studies and provided continuity to the netting program, as well as companionship and expertise in the field. Mr. R. Leong assisted with the field work and stomach analysis and also collected specimens during the winter. Mr. T. Jantzie ably assisted with the field work during the summer of 1972. Mr. D. Christiansen provided stimulating and helpful discussions with respect to the feeding behavior of fishes. Numerous Fish and Wildlife personnel participated in various aspects of this study and special thanks are due to Messrs. J. Allen and Chuck Scott for the many forms of help they offered.

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Ms. Anne Krawciw assisted with the preparation of the final draft of the manuscript.

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## Introduction

During May of 1970, coho salmon (Oncorhynchus kisutch) were introduced into Cold Lake, Alberta, via the Medley River, with the hope of providing a significant stimulus to the sport fishery in the area northeast of Edmonton. This area is well endowed with lakes, many of which provide excellent fishing for northern pike (Esox lucius) and walleye (Stizostedion vitreum), while in Cold Lake, only a limited sport fishery for these species exists. Indiscriminate harvesting had led to a severe reduction of the once-abundant lake trout (Salvelinus namaycush) by the late 1930's and the once-famous fishery for this species declined. Miller (1956) demonstrated that the lake trout in Cold Lake were slow growing and late maturing, thus easily depleted due to their slow replacement. Closure of Cold Lake to commercial fishing following Miller's report eliminated a significant source of depletion of lake trout stocks and there were signs that the lake trout were becoming more abundant. Since 1965 young lake trout have been introduced into Cold Lake annually to supplement natural recruitment, which was either inadequate to maintain the population or resulted in only slow recovery of its numbers. Inadequate recruitment may have been due to the "significant residues" of DDT which were found in lake trout, from Cold Lake (Paetz and Zelt, 1974). Burdick et al (1964) demonstrated detrimental effects of DDT on hatching success and survival of lake trout eggs.

Introduced coho salmon in the Great Lakes grew to a size of 12-15 lb (5.44 - 6.81 kg) in two years by preying extensively upon the abundant alewives (Alosa psuedoharengus) found there. It was hoped that similar success might result in Cold Lake where abundant cisco (Coregonus artedii) are found. The initial introduction of coho salmon into Cold Lake was made possible by the gift to the Province of Alberta, from the State of Alaska, of 100,000 eyed eggs, in 1968. These were hatched in the hatchery in Calgary, raised for one year at the Raven Rearing Station and in May of 1970, early in the second year of their lives, they were brought to a holding pond along the Medley River from which they were released. Introductions were also made in 1971 and 1972.

The rationale behind the introductions are discussed in Buchwald (1971) while their mechanics are discussed by Moller (1972). During 1970, netting results indicated that coho salmon were widely distributed throughout Cold Lake. During late summer a large return of precocious male salmon (jacks) to the Medley River provided evidence that imprinting (sensu Carlin, in Hasler, 1966), to the water into which they had been introduced, had been successful and that growth and survival were good during the first summer at least. A study to determine space and food utilization of the introduced coho salmon and native piscivorous fishes was undertaken during the summers of 1971 and 1972. Specimens were taken largely by means of gill-netting.

Frequently, feeding studies of predaceous organisms merely present a list of what food items were found within the stomachs of the predators. This in itself provides little predictive information and such studies are of little comparative value. By examining the distribution and behavior of both predator and prey an attempt can be made to account for differences in the feeding within a species over a period of time, and between species at a given time. This has been the underlying philosophy of the present work at Cold Lake, providing the basis for assessing the impact upon the native fish fauna of the introduced coho salmon, and the effects of the native fishes upon the success of this exotic species in its new environment.

The specific objectives of this study are as follows:

(1) to describe the distribution and diet of coho salmon in Cold Lake;

(2) to describe the distributions and diets of the native piscivorous fishes, with emphasis on those species in contact with the coho salmon;

(3) to describe the distribution of other species of fish that might interact with coho salmon;

(4) to compare the utilization of forage fish between coho salmon and the native piscivorous fishes;

(5) to assess the role of interactions with the native fishes upon the success of coho salmon.

A study of the parasites of the fishes of Cold Lake was undertaken concurrently by Mr. Ray Leong, of the University of Alberta, to determine the effects of parasites on the success of coho salmon in Cold Lake.

## Description of the Study Area

The geographical location, morphometry, physical and chemical characteristics of Cold Lake, Alberta, (figure 1) are described in Paetz and Zelt (1974). Of particular significance are its depth (maximum 112 m, mean 51.8 m), sparse vegetation (Appendix I), and low shoreline, exposing the lake surface to the wind. The contours of the lake basin are irregular with a gradual increase in depth in North and English Bays, while much of the eastern and south-eastern portions of the lake are characterized by a rapid increase in depth (figure 2). The surface temperature rarely exceeds 20°C and the depth at which given isotherms in the metalimnion are found during the summer is highly variable (figure 3), especially in North and English Bays. Water warmer than 15°C is rarely encountered at depths greater than 15 m during August or early September, the time at which the maximum penetration of this isotherm is realized.

Cold Lake contains a greater number of fish species than any other lake in Alberta (Roberts, 1973) and includes 22

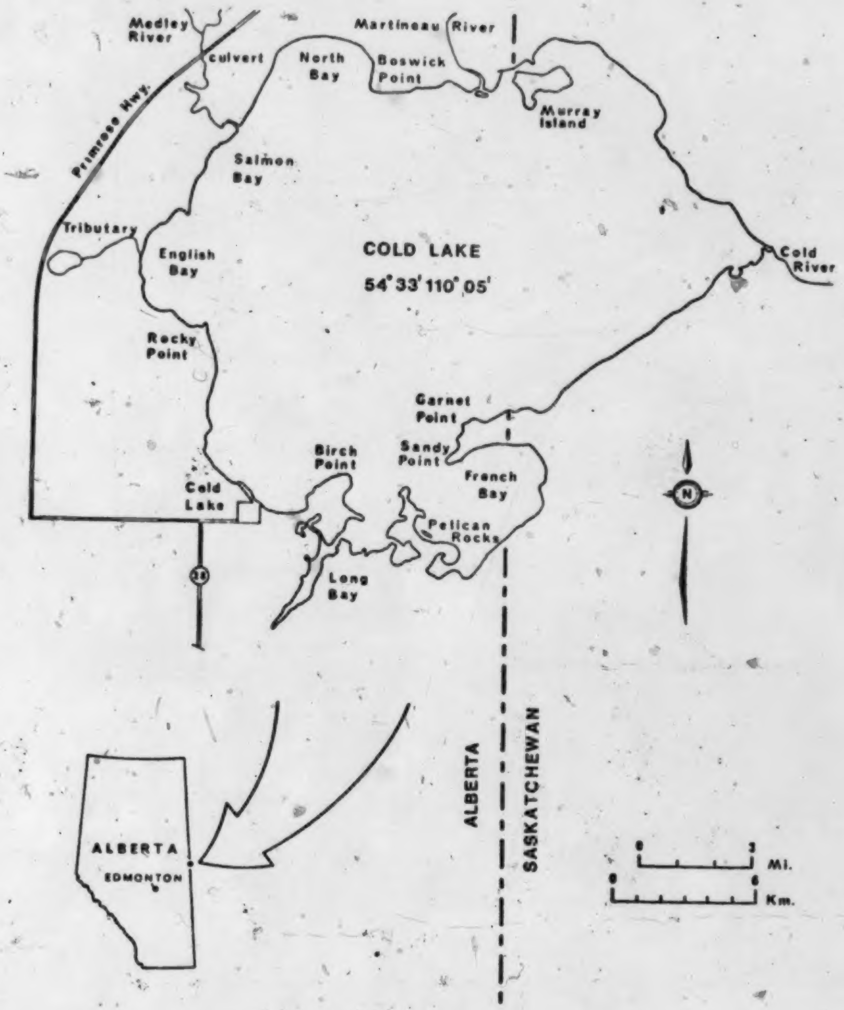

Medley River
culvert
Primrose Hwy.
North Bay
Martineau River
Boswick Point
Murray Island
Salmon Bay
Tributary
English Bay
COLD LAKE
54°33' 110°05'
Cold River
Rocky Point
Garnet Point
Sandy Point
Birch Point
French Bay
Cold Lake
Pelican Rocks
28
Long Bay
N
ALBERTA
EDMONTON
ALBERTA
SASKATCHEWAN
0
3
Mi.
0
5
Km.

Figure 1. General features of Cold Lake.

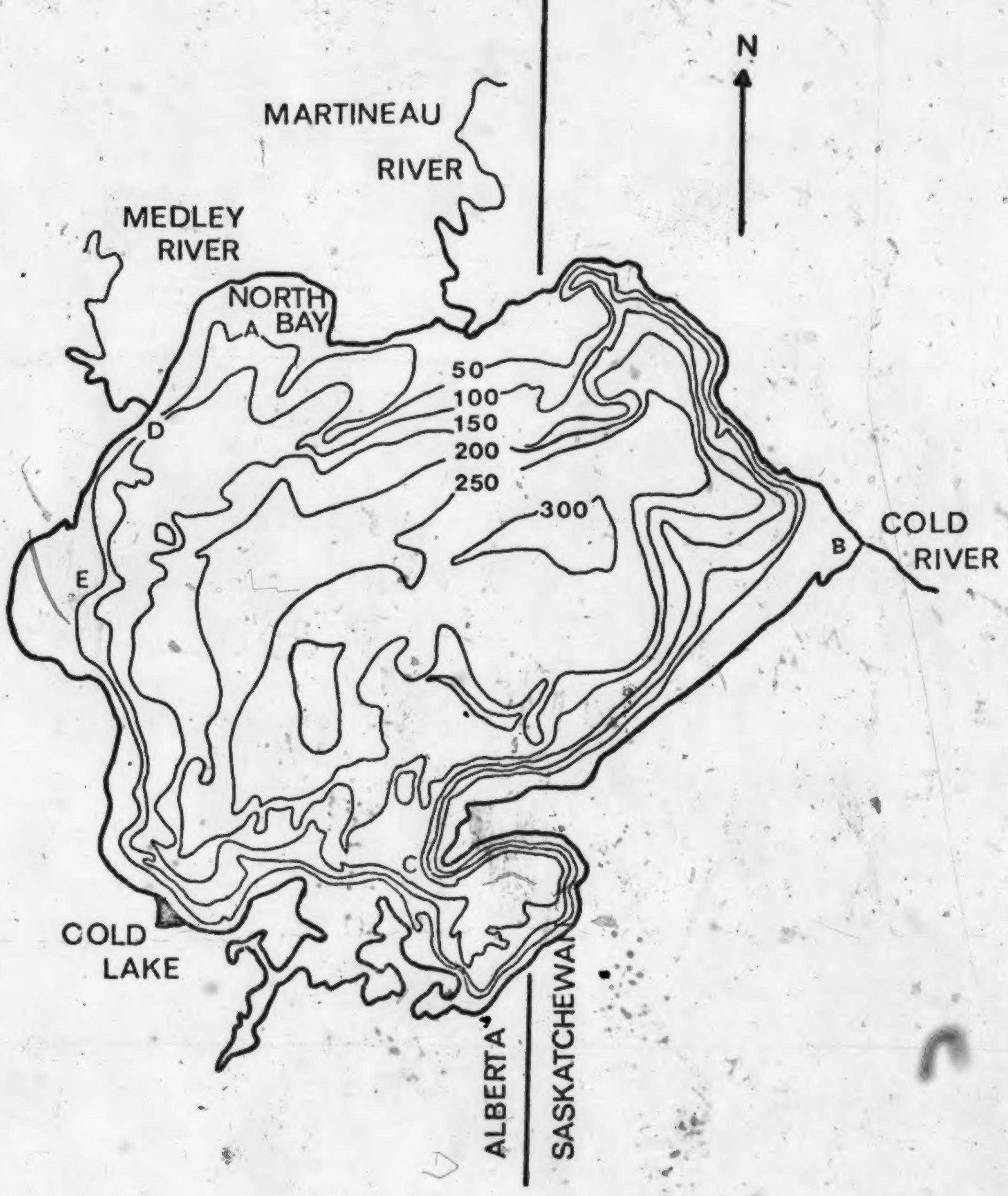

N
MARTINEAU
RIVER
MEDLEY
RIVER
NORTH
BAY
A
50
100
150
200
250
300
D
D
E
B
C
COLD
RIVER
COLD
LAKE
ALBERTA
SASKATCHEWAN

Figure 2. Bathymetric map of Cold Lake.
(After Paetz,1972).

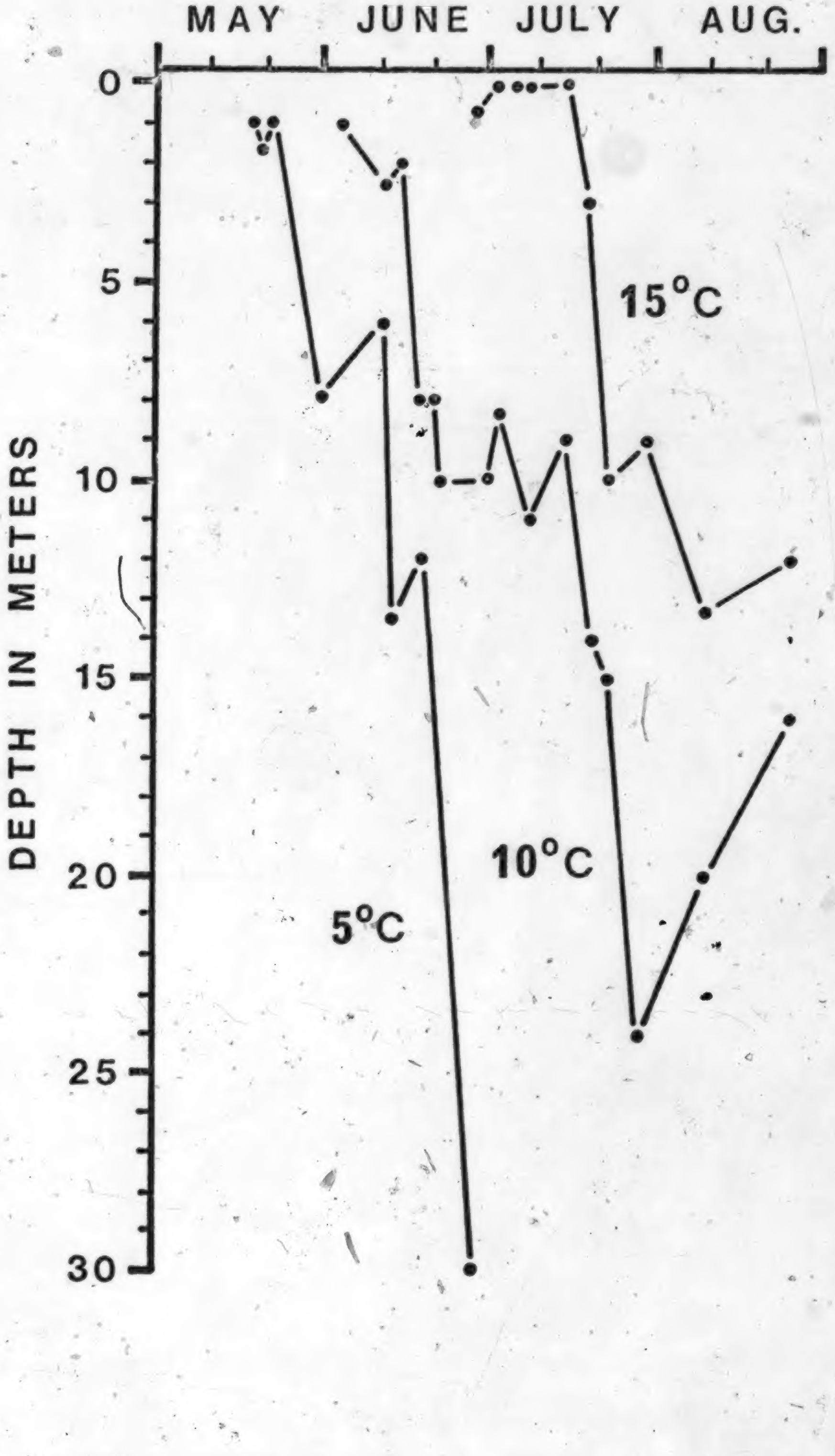


Figure 3. Depths at which selected isotherms occurred in Cold Lake, May-August, 1971.

Table 1. Species of fish and their relative abundance in Cold Lake[a].

| | | |
|---|---|---|
| *Thymallus arcticus* (Pallas)[b] | arctic grayling | I- |
| *Coregonus clupeaformis* (Mitchill) | lake whitefish | +++ |
| *Coregonus artedii* Lesueur | cisco | ++++ |
| *Salvelinus namaycush* (Walbaum) | lake trout | ++ |
| *Salmo gairdneri* Richardson | rainbow trout | I+ |
| *Oncorhynchus kisutch* (Walbaum)[c] | coho salmon | I++ |
| *Esox lucius* Linnaeus | northern pike | +++ |
| *Couesius plumbeus* (Agassiz) | lake chub | ++ |
| *Notropis hudsonius* (Clinton) | spottail shiner | +++ |
| *Notropis atherinoides* Rafinesque | emerald shiner | ++ |
| *Pimephales promelas* Rafinesque | fathead minnow | ++ |
| *Chrosomus neogaeus* (Cope) | finescale dace | + |
| *Semotilus margarita* (Cope) | pearl dace | + |
| *Rhinichthys cataractae* (Valenciennes) | longnose dace | + |
| *Catostomus catostomus* (Forster) | longnose sucker | ++ |
| *Catostomus commersoni* (Lacepede) | white sucker | +++ |
| *Percopsis omiscomaycus* (Walbaum) | trout-perch | + |
| *Lota lota* (Linnaeus) | burbot | +++ |
| *Culaea inconstans* (Kirtland) | brook stickleback | + |
| *Pungitius pungitius* (Linnaeus) | ninespine stickleback | ++++ |
| *Etheostoma exile* (Girard) | Iowa darter | + |
| *Perca flavescens* (Mitchill) | yellow perch | ++ |
| *Percina caprodes* (Rafinesque) | logperch | + |
| *Stizostedion vitreum* (Mitchill) | walleye | ++ |
| *Cottus cognatus* Richardson | slimy sculpin | ++ |

[a] I Introduced; - Not present; + Rare; ++ Common; +++ Abundant; ++++ Very abundant.

[b] Unsuccessful introduction (Medley River).

[c] 1970-1973.

native species and three exotics, one of which, the arctic grayling (Thymallus arcticus) introduced into the Medley River during 1964, failed to establish itself and is not maintained by stocking. The fishes of Cold Lake are listed in Table 1, along with estimates of their relative abundance. Piscivorous waterfowl observed at Cold Lake, either as migrants or residents, are listed in Appendix II.

The southern half of Long Bay and the shallow weedy portions of French Bay were excluded from the study area. While they communicate with the main basin of the lake, they are distinct in their physical and chemical properties, their flora and their fauna.

## MATERIALS AND METHODS

Initial collections of coho salmon and other species of fish were made during the summer and fall of 1970, and January and February of 1971 by Mr. Knut Moller. During May to September of 1971 and 1972 fish collections and stomach analysis were done on a daily basis. During September of 1974, in conjunction with the Alberta Lakes Survey, the species and distribution of rooted aquatic and emergent vegetation were determined.

### Fish Collections

A total of 40,970 net-yard-nights (100 net-yard-nights = a 100 yard long gill-net set during the day and picked at the same time on the following day) gill-netting effort was utilized during the summers of 1970-1972 to collect fish. During 1971 gill-nets ranging from 254 mm to 140 mm (1" to 5 1/2") stretched mesh size were deployed in various depths in the water column and in various depths of water, throughout Cold Lake, in an attempt to capture salmon. Because nets set in water deeper than 12 m and mesh sizes larger than 3" failed to collect salmon, netting efforts during the latter part of 1971 and throughout 1972 were largely restricted to gill-nets of 3" stretched mesh or less deployed in water depths of 45' (13.7 m) or less. During the summer of 1972 gill-nets were set and picked on a daily basis immediately in front of the outlet stream, the Cold River, off the northwest tip of Sandy Point on and over a precipitous, rocky bottom and in Salmon Bay, southwest of the mouth of the Medley River. Nets at these stations were fished at different depths to determine the vertical distribution of the coho salmon. Other gill-nets were set for periods of approximately one week or more, in North, English and French Bays, while additional sets were made throughout the lake for a single night each. Gill-net sets usually consisted of two 50 yard lengths of net. A one inch stretched mesh monofilament was set in deep water, up to a maximum of 76 m, in an attempt to catch small benthic fishes such as cottids. Gill-netting was directed at catching coho salmon only, and other fish species were sampled as a by product of the salmon netting program. The differential susceptibility of different species, or different sizes of fish within a species, to capture by a particular mesh size of gill-net results in a non-random sample of the fish population. The relative abundance of each species based on such capture is not regarded as more than than a crude estimate.

Small fishes (potential forage fish) were collected with a common-sense seine along both sandy and rocky areas along the shoreline, and in or near the mouths of tributary streams. As with gill-netting, seining results in biased sampling and yields only a rough estimate of abundance. Galvanized wire minnow traps of 5 mm mesh, with one-way cone-shaped inlets at each end, were baited with fish eggs and deployed independently in water from 0.5 to 18 m deep, or attached to the harnesses of gill-nets. These traps selectively caught large male ninespine sticklebacks. Even though they were sometimes set in areas where other species occurred in abundance, they failed to catch more than the occasional cyprinid or sculpin.

Small fishes were identified and their abundance estimated by direct observation either from a boat or from the shore.

Knowledge of the distribution of small fishes was aided, although to a lesser extent, by examination of the stomach contents of piscivorous fishes.

## Measurements

The fork lengths of fish sampled were measured to the nearest millimeter. Weights of large fish were determined with a Chatillon spring balance, while those of specimens smaller than 1500 g were determined by a Pesola spring balance. The weights of forage species removed from fish stomachs were determined by weighing as many whole specimens as possible from each stomach and determining the mean weight.

The stomach contents of fishes were treated differently according to the feeding habits of each species. Food items from the mouth, oesophagus and stomach of a piscivorous fish were assigned from one to ten points, depending on their contribution to the total amount of food found within the pre-intestinal portion of the alimentary tract. The contribution of each food item was tabulated as a percentage of the total volume of the diet. The frequency of occurrence of each food item was recorded and expressed as a percentage occurrence in those stomachs containing food. Invertebrates were usually identified to at least the ordinal level, while fishes were identified to species whenever possible, and in the case of ninespine sticklebacks, the sex and reproductive state of adult individuals was determined. The fork lengths and number of individuals of each species of forage fish were also determined from each predator stomach examined. The stomachs of fish species that are not characteristically piscivorous were examined to determine if and when they ate fish. The diet of these fish was not recorded unless they were found to be eating fish, in which cases the species and number of forage fish ingested were recorded.

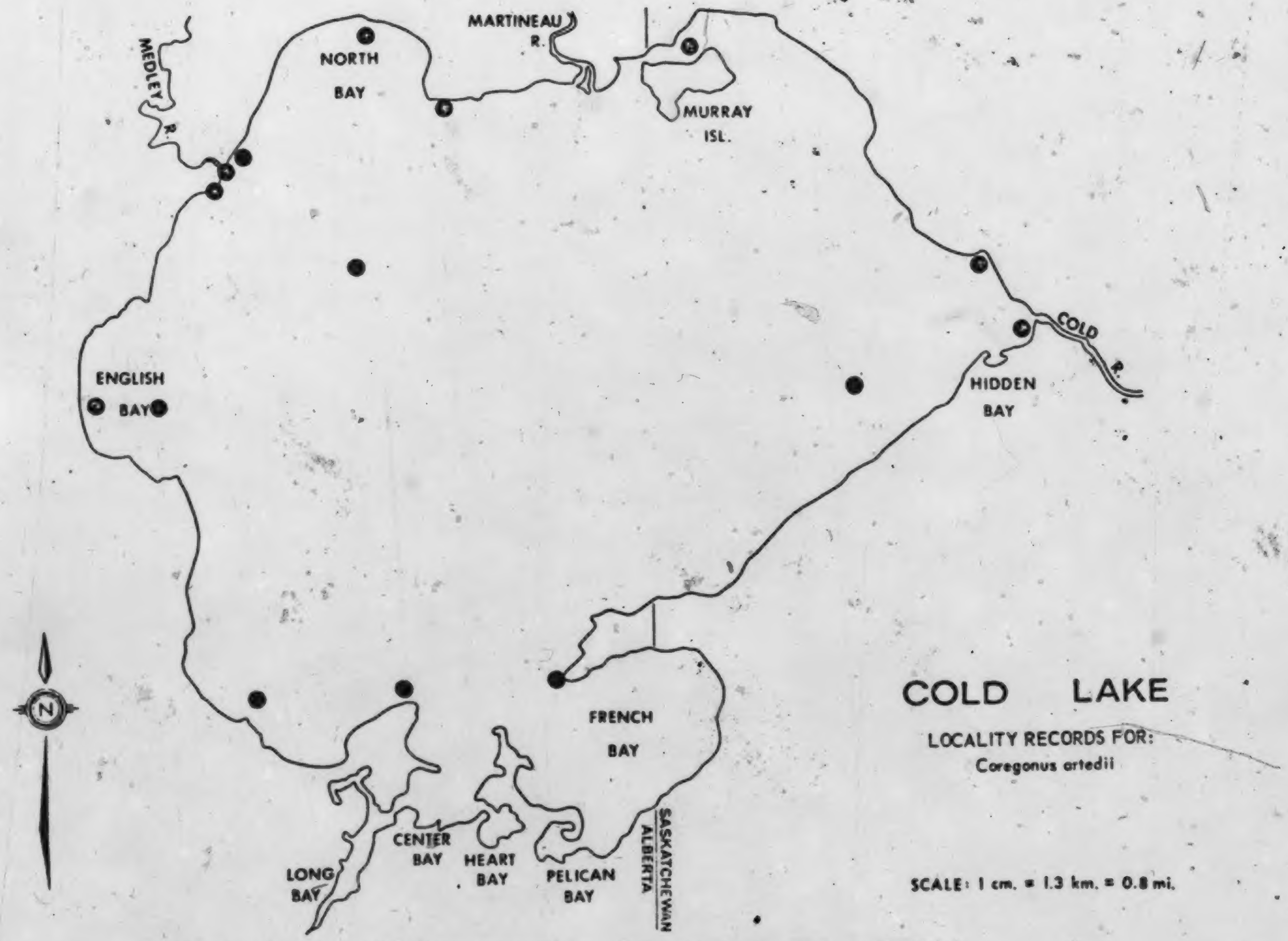
Partially digested fishes were identified by comparing them to cleared and stained specimens, the species of which were known. Stomach contents were examined immediately after removing the fish from the nets when possible, otherwise the stomach contents, or in the case of small specimens, the entire stomachs, were preserved in 10% formalin for later examination.

# RESULTS

The results of gill-netting during the summer of 1970, the winter of 1970-1971, and the summer of 1971 are summarized in Buchwald (1971), while those for the summer of 1972 are summarized in Moller (1972). The distributions of fishes and the food of each species are documented and discussed following the phyletic sequence of families in Bailey (1970). Nomenclature for both common and Latin names of fishes follows Bailey (1970) with the exception of the finescale dace, which is regarded as being in the genus Chrosomus by Paetz and Nelson (1970) and Scott and Crossman (1973). For the purposes of analysis and discussion shallow and deep water are regarded as being above and below the arbitrarily selected depth of 13.7 m (45') in Cold Lake.

## The Distribution of Cisco

Locality records for cisco in Cold Lake are shown in figure 4. This appears to be the most widespread and abundant of the fishes of Cold Lake. The vertical distribution of this species ranged from the surface to depths of at least 97.5 m, the greatest depth at which nets were set, with all portions of the water column being occupied. Gill-net catches at selected depths are shown in table 2 for the months May to September. The number of cisco taken in shallow water was low during the period from May to Septem-



MEDLEY R.
NORTH BAY
MARTINEAU R.
MURRAY ISL.
COLD R.
HIDDEN BAY
ENGLISH BAY
FRENCH BAY
LONG BAY
CENTER BAY
HEART BAY
PELICAN BAY
SASKATCHEWAN
ALBERTA
N
COLD LAKE
LOCALITY RECORDS FOR:
Coregonus artedii
SCALE: 1 cm. = 1.3 km. = 0.8 mi.

Figure 4 Locality records for Coregonus artedii

Table 2. Gill-net catches of cisco in less than 13.7 m. of water in Cold Lake during November 1970-November 1971, in fish/100 net-yard-night, total catch in parentheses.

| Nov.-Feb. | May-Sept. | October | November |
|---|---|---|---|
| 1154.4 (31,169) | 6.6 (485) | 40.6 (5481) | 623.3 (2190) |

Table 3. Gill-net catches of lake whitefish above and below 13.7 m. during May-September of 1970-1972.

| Depth | May | June | July | August | September | Year |
|---|---|---|---|---|---|---|
| >13.7 m. | — | 14.5 (29) | 8.6 (62) | — | — | 1970 |
| <13.7 m. | — | 14.0 (14) | 18.8 (199) | — | — | |
| >13.7 m. | 7.3(22) | 19.1 (386) | 6.2 (118) | 1.0 (35) | 3.9 (93) | 1971 |
| <13.7 m. | — | 23.0 (75) | 11.0 (55) | 10.2 (92) | 7.2 (43) | |
| >13.7 m. | 8.0 | 9.4 (546) | 1.7 (93) | 0.8 (46) | 1.4 (5) | 1972 |
| <13.7 m. | — | 10.0 (30) | 12.4 (81) | 4.5 (52) | 40.6 (61) | |

ber and increased in October. Maximum catches in shallow water occur during November and December.

Discussion

Cisco appear to occupy all of the study area in Cold Lake, at least during some portion of the year. With one exception, all cisco taken in gill-nets were age class 1+ (rare) or older. The distribution of young of the year cisco is uncertain but they are probably pelagic in rather deep water. Cisco are probably more numerous than indicated by netting returns because many would pass through the meshes of all but the smallest mesh (3/4" - 1 1/2") net due to their small size. Miller (1956) found the average size to be 0.16 lb (20-25 mm fork length) in Cold Lake.

During May cisco were taken at all depths of Cold Lake but as the lake warmed they became less common in the shallows. Engel (1972) found that the median temperatures at which cisco were caught in Palette Lake, Wisconsin, during each of three consecutive years were 10.9, 9.7 and 10.2 C and suggested that the upper limit of their vertical distributions was limited by their avoidance of warm water. Colby and Brooke (1969) found that cisco in two Michigan lakes occupied the metalimnion during the summer in a "cisco layer" bounded above by a temperature of 20°C. The surface waters of Cold Lake are only 20 C or greater during the month of August and are not constantly above this level. Water at

20 C is seldom encountered more than 5 m below the surface thus no thermal barrier exists in Cold Lake to exclude cisco from the surface. Even during the warmest weather cisco were observed at the surface in the evening, and rarely during the day. At these times they appeared to be feeding, presumably on emerging insects or allochthonous material. For a short period they tolerated temperatures that they normally appear to avoid. Engel (1972) found evidence for vertical, diel movement of cisco only during the spring and fall overturns when the water is cooler than in summer, and notes that such migrations by coregonids are more common in northern European lakes than in their warmer North American counterparts.

During November cisco move into shallow water prior to spawning. The main spawning period is during the first two weeks of December (Paetz,1972) however ripe individuals are still evident in January (R. Leong, pers. comm.).

Young of the year cisco were apparently absent from the margin of the lake, where intensive collecting by means of seining, and setting fine mesh mono-filament gill nets and 1" gill nets yielded no specimens. Only one representative of this age class was collected during the years 1971-1974, a single specimen taken from 11 m of water, near the bottom in a large mesh gill-net. In Lake Ontario, young of the year cisco were found inshore, close to the shallow water spawning grounds where they hatched, and associated with young of the year lake whitefish (Pritchard,1930). As the young cisco grew they moved into deeper water and were absent from the lake margin by the time they had attained a length of about 20 mm. The aggregations of larval coregonids along the shore of Cold Lake appeared to be composed of lake whitefish only. The absence of young of the year cisco from shallow water may be due to pelagic spawning over deep water by the adults of this species. It has been assumed that they spawn in the shallows (Paetz,1972), because of the shoreward movement of the adults in the fall, in Cold Lake as in others. There appears to be no convincing evidence that they do spawn in shallow water in Cold Lake. Pelagic spawning by cisco has been noted in, or suggested as occurring in Lac Marquette (Koelz,1929) and Lake Superior (Smith, 1956; Dryer and Biel,1964). An inshore movement was noted prior to spawning in Lake Superior, but during the actual spawning the fish moved out into water up to 145 m deep, occupying depths from 9-12 m. Pelagic spawning may be advantageous in that the eggs settling in deep water are subject to warmer temperatures than they would be subjected to in the shallows, while they develop. Colby and Brooke (1970) found that cisco have a higher optimum temperature for development (5.6°C) than do lake whitefish (0.5°C). At 0.5°C cisco eggs required 236 days to 50% hatch, survival was low and abnormal development was high, slightly in excess of 20%. Wells (1966) found the larvae of one or more species of Coregonus at depths of 73 m in 91 m of water during mid-April in Lake Michigan. The earliest of these larvae appear to be C. artedi. Larval cisco were seen or collected near the surface over deep water in Lake Huron, and were not concentrated along the shore as were larval lake whitefish, although some cisco were taken here also (Faber, 1970).

## The Cisco as a Piscivore

Adult cisco feed mainly on plankton and large crustaceans, chironomid larvae and occasionally small fish (McPhail and Lindsey, 1970). A small number of cisco from moderately deep water in Cold Lake were examined and had only eaten invertebrates. Specimens taken in shallow water fed rarely on other than invertebrates, and only six of more than of 500 specimens examined during the present study [illegible]tained fish.

During June of 1972, 2 of 27 cisco taken from 13 m of water contained larval fish, presumably young cisco. Cisco taken near a whitefish hatchery outflow were found to contain an average of 275 larvae per stomach (Scott and Crossman, 1973). Such predation upon newly hatched coregonids may be a seasonal phenomenon of short duration, as cisco are not well adapted as piscivores and would have limited success seizing and retaining fish larger than these larvae and capable of stronger and faster swimming. In addition to their lack of morphological adaptations for catching and eating other fish the cisco of Cold Lake are limited in this pursuit by their small size which limits their swimming speed and the size of prey they can ingest.

The largest cisco collected during this study was 31.3 cm fork length, 420 g and 12 years old. This unusually large (for Cold Lake) specimen contained the remains of at least three young of the year ninespine sticklebacks. Three of 60 cisco examined during October of 1973 contained young of the year ninespine sticklebacks, one with 12 individuals, one with 10 and another with at least one. During late fall and early winter the shoreward movement of large numbers of adult ciscos prior to spawning would result in increased overlap of their distribution with that of ninespine sticklebacks and increase the potential for predation on the latter species by cisco. This potential is enhanced by the fact that both are cold water species and thus likely to be more active during the winter than are many other species of fish in Cold Lake. Examination of over 100 cisco stomachs during the winter of 1973-74 resulted in little evidence of such predation (R. Leong, pers. comm.). This was probably because cisco preyed upon organisms for which they are morphologically specialized.

## The Distribution of Lake Whitefish

Locality records for lake whitefish in Cold Lake are shown in figure 5. Young of the year and older age classes of this species were spatially segregated until August, the young occupying shallow inshore waters. Catches of lake whitefish at various depths are shown in table 3 for the months May-September. Approximately equal numbers were taken above and below 13.7 m in June, while in July and August catches in shallow water decreased. During and after September lake whitefish congregate in the shallows prior to spawning. This species was variously distributed throughout the water column from the surface to depths of at least 97.5 m and ranked second in terms of numbers of fish netted during this study.

## Discussion

It can be seen from figure 4 and table 3 that lake whitefish occupy all areas of the lake sampled. Miller (1956) found that from July to September, catches in 5 1/2" gill-nets were greatest at depths of about 30-45 m. The mean weight of his sample (3.45 lbs.) is larger than that for lake whitefish taken during the present study and the depth distribution of smaller individuals may differ. Rawson (1951) obtained maximum catches of this species at 10 m in Great Slave Lake. During June this species appears to be equally distributed in Cold Lake at the depths sampled but during July and August, as the shallow and surface waters become warmer, catches in shallow areas were low. The final

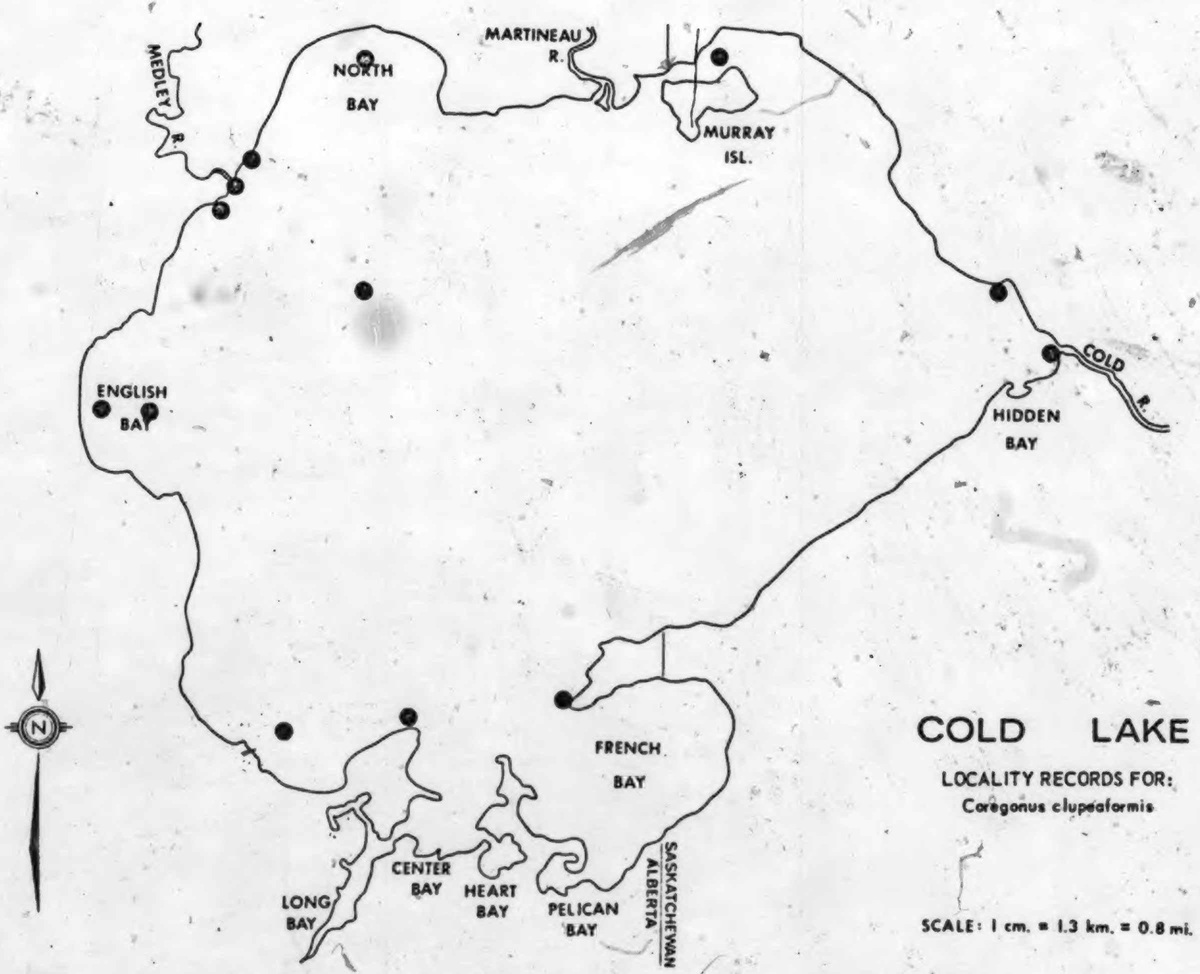

MEDLEY R.
NORTH BAY
MARTINEAU R.
MURRAY ISL.
COLD R.
HIDDEN BAY
ENGLISH BAY
N
FRENCH BAY
LONG BAY
CENTER BAY
HEART BAY
PELICAN BAY
SASKATCHEWAN
ALBERTA
COLD LAKE
LOCALITY RECORDS FOR:
Coregonus clupeaformis
SCALE: 1 cm. = 1.3 km. = 0.8 mi.

FIGURE 5 Locality records for Coregonus clupeaformis

temperature preferendum, and temperatures with which lake whitefish are associated in nature are 12.7°C and 11.4 - 11.9°C respectively (Ferguson, 1958). These temperatures were found near the surface in early July but only at depths in excess of 15 m by the end of this month. The abundance of adults in shallow water was at a maximum during November, at which time spawning beds, a major one described by Paetz (1972) located in 2 to 4 m of water, are occupied. Lake whitefish also enter the Martineau and Medley Rivers, progressing upstream as far as the Primrose highway, for the purpose of spawning (C. W. Scott, pers. comm.).

The maximum depth at which lake whitefish were taken during this study, 98 m, is consistent with the findings of Rawson (1951), however this species is known to occur at depths of 128 m in the Great Lakes (Scott and Crossman, 1973).

Young of the year lake whitefish were evident on May 16, 1972, by which time the ice had receded about 300 m from shore in North Bay. The larvae were 15-17 mm long and actively feeding on plankton near the surface within 1 m of the shore. They probably migrated to the lake margin from spawning sites near by. Faber (1970) concluded that lake whitefish in Lake Huron migrated to the shore from a near or distant spawning ground because the larvae were present as well developed, rather than newly hatched individuals, when they first appeared and were collected along the lake margin. Rawson (1951) found young lake whitefish to be distributed along the shore in Great Slave Lake. During subsequent months young of the year lake whitefish remained near the shore and were seen at other similar sites around the margin of Cold Lake. At night they were found within 15-30 cm of the shore possibly as a defense against predation by fish. During periods of intense wave action they moved into deeper water. By August, as they grew larger, they moved further from shore but remained within 4 to 5 m of it, in depths of up to 2 m. During late August and early September they were taken in 1" gill-nets, near the bottom, at depths of up to 13 m. Reckahn (1970) found that the distribution of young of the year lake whitefish in Lake Huron was in close association with the 17°C isotherm, which, in Cold Lake, is located in the top 1 m of water, descending gradually throughout the summer, until it attains a maximum depth in excess of 7 m in August. In Lake Huron, after 6 to 8 weeks in the metalimnion, the top of which is near the 17°C isotherm, the young lake whitefish move into deep water.

While older whitefish are considered to be schooling fish, the aggregations of larvae do not constitute schools as defined by Keenleyside (1955). Faber (1970) supports this view. As the summer progressed the growing whitefish were observed to swim in small schools distinct from the aggregation of fishes along the shore with which they were associated earlier.

## The Lake Whitefish as a Piscivore

The lake whitefish generally includes few fish in its diet and generally preys extensively upon invertebrates. In Lake Athabasca and Great Slave Lake Pontoporeia affinis makes up over half the diet (McPhail and Lindsey, 1970), and in Cold Lake it is the most important food item of this species. The only species of fish identified from the stomachs of lake whitefish during this study was the ninespine stickleback. Predation by lake whitefish upon ninespine sticklebacks was most common during June, at which time both species are common in shallow water. Eleven of 73 specimens of lake whitefish in excess of 400 mm fork length contained from 1 to 39 ($\bar{x}$ = 15.4) ninespine sticklebacks, either as their exclusive food, or in combination with fish eggs. Stomachs containing fish eggs contained from 1 to 3 fish, while 2 stomachs, in which fish were the only food items, contained 33 and 39 ninespine sticklebacks. All sticklebacks appeared to be mature adults, ranging from 43-63 mm fork length ($\bar{x}$ = 54 mm) and of 31 specimens sufficiently intact to determine the sex, 8 were males and 23 were females. The apparent selection of large ninespine sticklebacks may reflect the make-up of the adult aggregations from which they were taken and the relative ease of capture of egg laden females. The absence of female sticklebacks in excess of 65 mm may be owing to their relative lack of abundance, or the difficulty of swallowing large individuals.

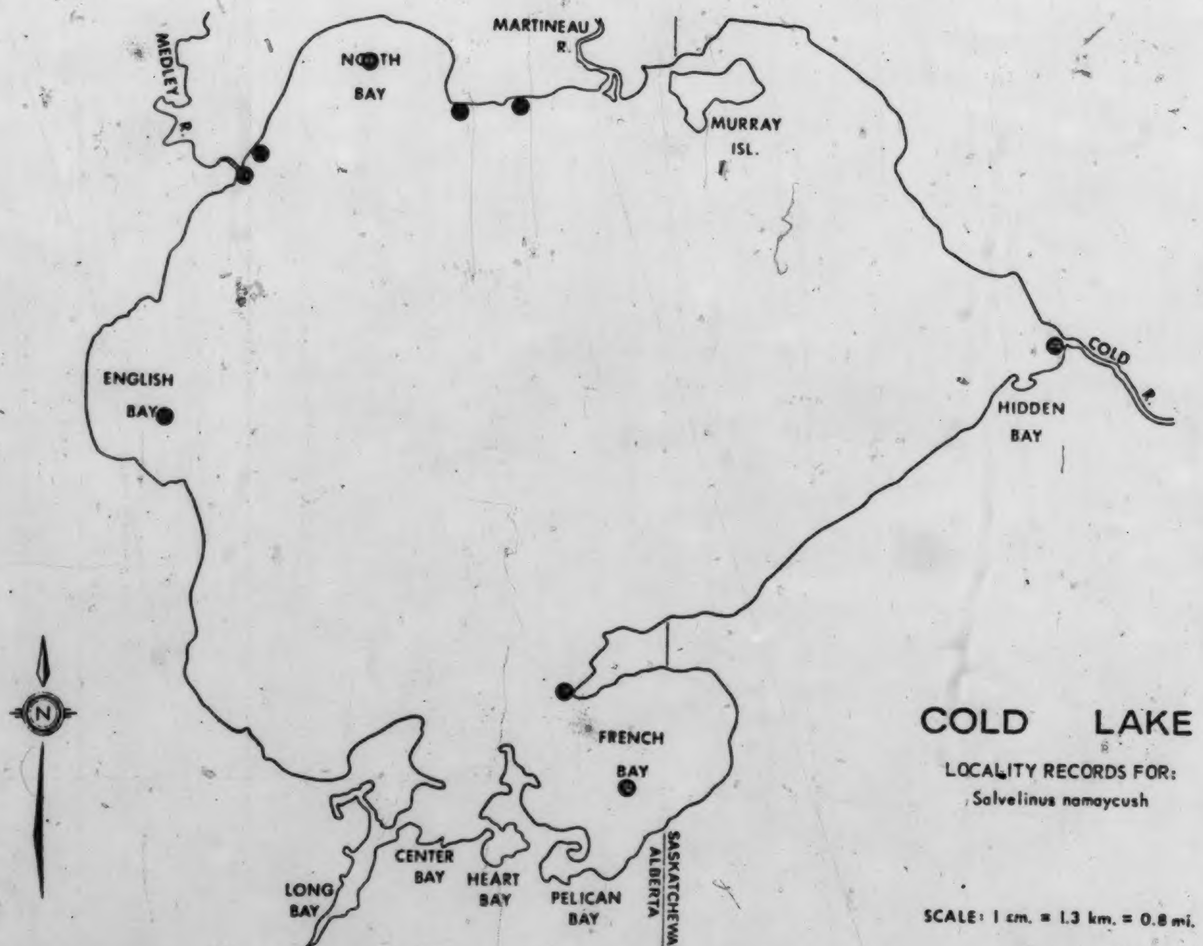
Perhaps the spines of large sticklebacks are a deterrent to this predator. Predation upon ninespine sticklebacks at other times of the year appears uncommon but occasionally specimens taken during the winter contain adults, subadults and some young of the year.

Utilization of fish by lake whitefish has been noted in a number of studies reviewed by Scott and Crossman (1973). Ninespine sticklebacks were the only fish identified from lake whitefish stomachs in Kakisa Lake, N.W.T. (D. Christiansen, pers. comm.). Bidgood (1972) and Ash (1974) noted predation upon young of the year yellow perch in Pigeon and Wabamun Lakes, respectively. In Lake Wabamun this occurred during the fall when the small yellow perch were moving into deeper water and the lake whitefish were moving into the shallows, their distributions during the summer overlapping only slightly or not at all.

The utilization of food other than fish was not documented during this study. However it was noted that some individual lake whitefish appeared to specialize in particular prey types, the food of an individual being exclusively composed of, or dominated by, a particular prey item such as Pontoporeia, sphaeriid clams, phryganeid caddis flies, fish eggs or occasionally fish. Other individuals taken at the same time and place were specializing in different food items or contained a variety of foods. Short term individual specialization might arise as the result of rapid learning and the formation of a search image. Two possible advantages of this might be an increase in feeding efficiency and reduction of intraspecific competition. The impact of such a phenomenon on forage fish is illustrated by the large numbers of ninespine sticklebacks eaten by lake whitefish. Lake whitefish are smaller than the characteristically piscivorous fishes, and generally prey upon invertebrates. Lake whitefish are sufficiently numerous to act as significant predators of small fish, at least of those species or their developmental stages that are sufficiently small, slow swimming, or lack effective defense mechanisms. Bidgood (1972) suggests that by preying upon the young of the year walleye, lake whitefish contributed to the decline of this species in Pigeon Lake. In Cold Lake the young of the year of most species of fish are not in contact with adult lake whitefish, and although other factors may be important for maintaining this segregation, it may be reinforced by the presence of this potential piscivore.

## The Distribution of Lake Trout

Locality records for lake trout are shown in figure 6. Adult lake trout are generally distributed throughout the lake during the winter but seem to be concentrated near the lake margin in early summer until mid or late July, after which they are found in deep water throughout the lake. Movement to spawning areas in shallow water,



MEDLEY R.
NORTH BAY
MARTINEAU R.
MURRAY ISL.
ENGLISH BAY
COLD R.
HIDDEN BAY
FRENCH BAY
LONG BAY
CENTER BAY
HEART BAY
PELICAN BAY
SASKATCHEWAN
ALBERTA
N
COLD LAKE
LOCALITY RECORDS FOR:
Salvelinus namaycush
SCALE: 1 cm. = 1.3 km. = 0.8 mi.

FIGURE 6 Locality records for Salvelinus namaycush

such as the rock-bottomed area near the outlet stream, occurs during September and October. Lake trout were taken at depths ranging from 1 m below the surface in 2 m of water to near the bottom in 97.5 m (320'). No young of the year were collected but sub-adult individuals of age classes II$^+$ and III$^+$ were encountered in moderately deep water to a maximum depth of 36.5 m (120'). Water temperatures at the depths at which lake trout were captured were always less than 15 C.

Lake trout do not appear to be abundant in Cold Lake, only 92 specimens being taken during netting during the three summers of this study.

## Discussion

Lake trout have the greatest vertical and horizontal distribution among the piscivorous fishes of Cold Lake, the extents of both reaching a maximum during the winter months. During the winter they may be taken from "all depths" during the commercial fishery (Miller, 1956). Immediately following break up lake trout appear to be concentrated in the littoral zone. During June of 1970 and 1971, 18 lake trout were taken in less than 13.7 m (45') of water, while with equal fishing intensity at depths greater than this, only 4 specimens were taken. During June of 1972, 20 lake trout were taken in shallow water while none were taken at depths exceeding 13.7 m. Shallow water angling for lake trout was observed to be generally successful until at least late June. Miller (1956) documents similar shallow water angling success for lake trout during the early portion of the open water season at Cold Lake. Scott and Crossman (1973) note that lake trout generally frequent the surface waters of lakes immediately after break up. In July as the epilimnion warms lake trout move into deeper water. Catches of lake trout in shallow water during July declined while those for deeper water increased. Miller (1956) observed that lake trout in Cold Lake tended to avoid water warmer than 10°C. The preferred temperature of this species ranges from 8 - 15.5°C (Ferguson, 1958). This temperature range is characteristic of the littoral zone of Cold Lake until near the end of July. Of a total of 22 lake trout caught during August of the years 1970-72, 21 were taken at depths in excess of 13.7 m. The single shallow water specimen was taken from water 2 m deep immediately in front of the outlet stream, during a period when effluent water was cooler than water of similar depth throughout the lake (see figure 7).

During, and after September, lake trout are concentrated in those shallow water areas with cobble-boulder substrate, for the purpose of spawning (Knut Moller, pers. comm.). The sites of egg deposition are only occupied at night, the lake trout apparently moving to adjacent, deeper areas during the day. The duration of the spawning period has not been determined but may be expected to be from 10

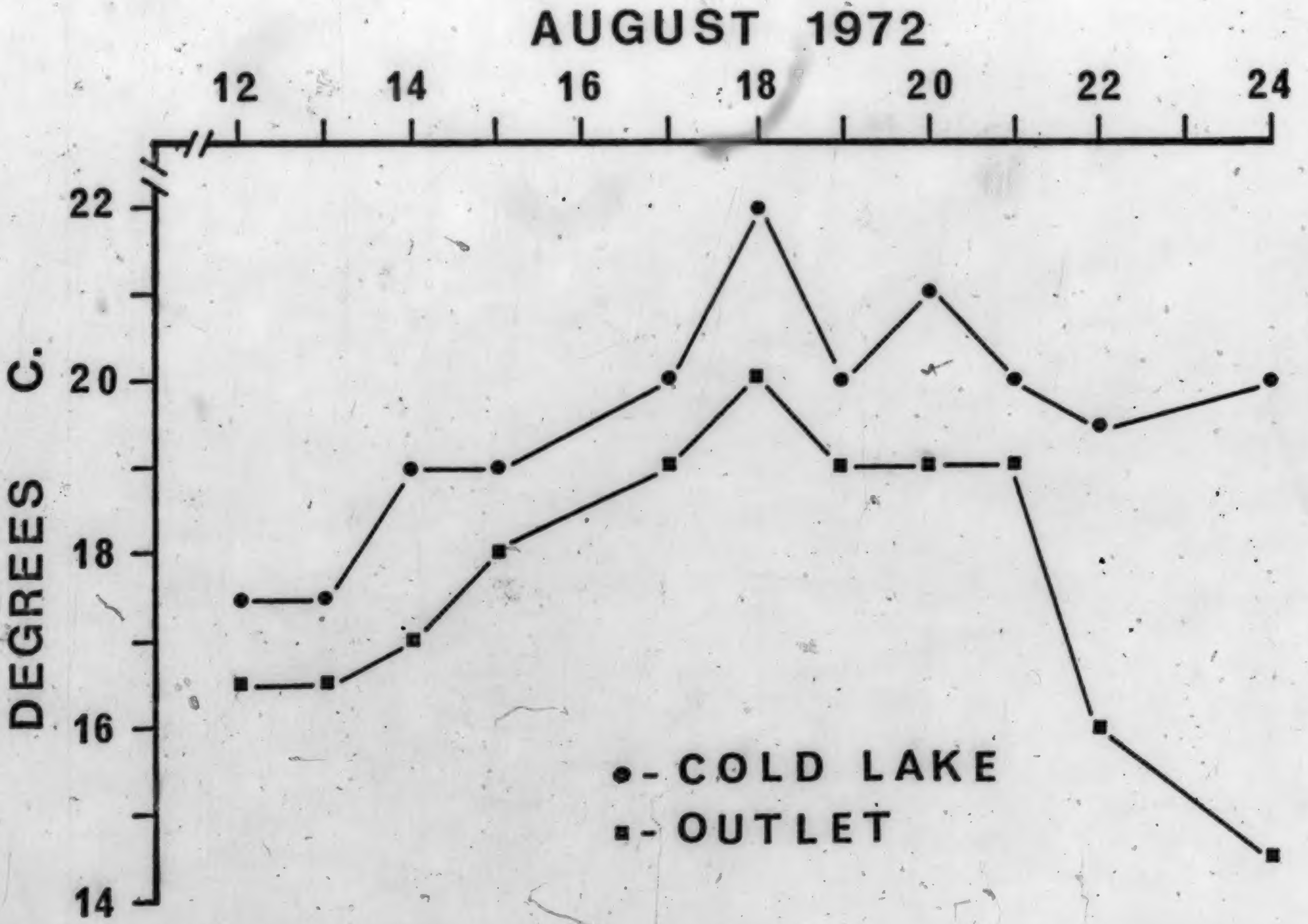


Figure 7. Surface temperatures in ° C of Cold Lake and the Cold River at the outlet. (August 12-24, 1972)

days to 2 weeks as in other areas (Martin, 1957; Rawson, 1961). Miller (1956) notes that spawning is finished by late October, at which time, they may be taken by angling in shallow water. Slow dispersal occurs following spawning, giving rise to the general distribution of this species throughout Cold Lake.

The upper limit of the vertical distribution of lake trout in Cold Lake appears to coincide with the depth of the 15°C isotherm.

## The Food of Lake Trout

### Results

The stomach contents of 37 lake trout are listed in table 4. Fish were the only food items encountered and consisted of only 2 species, ciscoes and ninespine sticklebacks. Only a single juvenile lake trout was examined, the remainder being adult and large sub-adult individuals. Seventy-five percent of the lake trout with food in their stomachs caught in deep water had eaten ciscoes; the remainder containing sticklebacks. In contrast, only 14.3% of the shallow water specimens contained ciscoes and 85.7% contained sticklebacks.

Ciscoes removed from lake trout stomachs were sub-adult or adult individuals of 15 cm or greater fork length. All sticklebacks examined from lake trout stomachs were adults, most of which were large, ripe females. The mean number of prey items per 10 cm length class appears to

Table 4. Stomach contents of 37 lake trout caught in Cold Lake, May-September, 1972.

| Size of predator | Depth of capture | | Number and species of prey | |
|---|---|---|---|---|
| (10 cm fork length class) | 13.7m | 13.7m | ninespine stickleback | cisco |
| 3 | + | | 5 | - |
| 4 | + | | 1 | - |
| 4 | + | | 1 | - |
| 4 | + | | 10 | - |
| 4 | + | | 28 | - |
| 4 | + | | empty | |
| 5 | + | | 56 | - |
| 5 | + | | 18 | - |
| 5 | + | | 30 | - |
| 5 | + | | 4 | - |
| 5 | + | | 20 | - |
| 5 | + | | 1 | - |
| 5 | + | | 9 | - |
| 5 | + | | 45 | - |
| 5 | + | | empty | |
| 6 | + | | 29 | - |
| 6 | + | | 10 | - |
| 6 | + | | 60 | - |
| 6 | + | | 6+* | - |
| 6 | + | | - | 2 |
| 6 | + | | 67 | - |
| 6 | + | | empty | |
| 7 | + | | - | 2 |
| 7 | + | | - | 2 |
| 2 | | + | 1 | - |
| 4 | | + | 5 | - |
| 4 | | + | - | 2 |
| 5 | | + | 38 | - |
| 5 | | + | - | 4 |
| 6 | | +(67m)** | 8 | - |
| 6 | | + | empty | |
| 6 | | + | - | 1 |
| ? | | + | - | 2 |
| ? | | + | - | 4 |
| ? | | + | - | 3 |
| ? | | + | - | 3 |
| ? | | + | - | 5 |

* An undetermined number of sticklebacks were regurgitated while the lake trout was still in the water.

** Maximum depth at which ninespine sticklebacks were noted during the present study.

increase with increasing predator size when the 40, 50 and 60 cm length classes are compared (see table 4).

## Discussion

The diet of adult lake trout in Cold Lake is notable for a number of reasons. Apparently only two of the potential forage fish species are utilized. Examination of a larger number of lake trout stomachs might reveal the inclusion of other species; however the data presented in table 4 are consistent with observations made in 1971.

Cisco have been noted as an important forage fish for lake trout in many populations (Rawson,1961; Dryer et al,1965; Martin,1970). In Cold Lake the distributions of lake trout and cisco are very similar. This similarity, combined with the abundance of cisco enhances their potential as a forage fish for lake trout. Sticklebacks appear to be available to lake trout in a somewhat similar fashion, but become more so during May-July when dense aggregations of adult sticklebacks are found in shallow water along the lake margin. Although cisco and other species of potential forage fish are available during this period, lake trout appear to prey selectively on sticklebacks, perhaps owing to their ease of capture, especially in the case of ripe female individuals swollen with eggs. A search image for sticklebacks may be formed by the lake trout at this time, serving to increase their efficiency as predators upon this species, and resulting in their ignoring other potential prey species. The seasonal superabundance of potential forage fish along the lake margin may in part explain the shoreward movement of lake trout at this time. Such a prey-oriented movement has been suggested for rainbow trout (Salmo gairdneri) feeding on redside shiners (Richardsonius balteatus) in Paul Lake, B.C. by Crossman (1959).

Lake whitefish are apparently not utilized as food by adult lake trout in Cold Lake, however they may be expected to be found in low numbers during examination of a large number of stomachs. It is of interest that lake whitefish decreased in importance as a forage fish for lake trout in Lake Opeongo, Ontario, following the introduction of cisco (Martin, 1970). This may have been due to the relative abundance of these two coregonids and/or that cisco are frequently encountered in dense schools. Whitefish of the size range 15-25 cm are far less numerous than cisco of the same size range in Cold Lake and are encountered in smaller, less dense aggregations. Young of the year lake whitefish in Cold Lake occupy very shallow water along the lake margin until late in their first summer of life and are thus not in contact with lake trout.

Other forage fish species that are important diet items of lake trout in other areas, but not in Cold Lake include sculpins, yellow perch, and troutperch. Sculpins were an important diet item of lake trout in Lake Michigan (Van Oosten and Deason, 1938) and Lac La Ronge, Sask. (Rawson, 1961). Their absence in the diet of lake trout in Cold Lake may be due, in part, to their being located most frequently among large boulders or otherwise coarse substrate and thus less accessible than are limnetic forage species. Yellow perch were formerly the most important forage fish for lake trout in Lake Opeongo (Martin, 1970) but the distributions of these two species in Cold Lake appear not to overlap (figures 6 and 14) and there is thus little opportunity for predation on yellow perch by lake trout. Trout-perch appear to be rare in Cold Lake and perhaps not encountered frequently by lake trout, while in other areas they are more abundant and utilized by lake trout (McPhail and Lindsey, 1970; Scott and Crossman, 1973).

Cannibalism has been noted among lake trout in the absence of other potential forage fish (McPhail and Lindsey, 1970), but is infrequent in Lake Opeongo, where only eleven lake trout were contained in 17,000 stomachs examined (Martin, 1970). It is probably insignificant in waters with sufficient forage fish, including Cold Lake.

Invertebrates are not generally important in the diet of adult lake trout, but were the dominant food items of this species in Lake Louisa, Ontario, during the summer (Martin, 1970) and throughout the year in Swan Lake, Alberta, (Paterson, 1968), in both cases owing to the reduced availability of forage fish. The opossum shrimp (Mysis relicta) and the amphipod Pontoporeia affinis may be important in the diet of young lake trout in Cold Lake as they are in other lakes (McPhail and Lindsey,1970; Scott and Crossman,1973).

Lake trout that had eaten cisco contained two to five individuals from within a narrow (15-25 cm fork length) size range. Both large and small lake trout ate cisco of similar size, that is, there was no apparent increase in prey size with increase in predator size. Too few lake trout were examined to determine whether the number of cisco eaten increased with increasing predator size. The mean numbers of ninespine sticklebacks per stomach for 40, 50, and 60 cm fork length classes were 9, 21.3, and 30, reflecting an increase in number of prey eaten with increasing predator size. Martin (1970) found that rather than eating more individuals of a prey species, larger lake trout in Lake Opeongo ate larger individuals. Since the sticklebacks preyed upon by lake trout in Cold Lake are close to the maximum size available for this species (in Cold Lake), the increase in numbers eaten per predator seems predictable in the absence of switching to alternate prey.

Empty stomachs in lake trout were not encountered with great frequency at any particular time and only four of 37 stomachs examined during the summer of 1972 were empty. Martin (1952) and Paterson (1968) found few empty stomachs in lake trout during the summer, but their frequency increased and reached a peak in the fall. Lake trout can not be caught by angling during spawning time (Miller, 1956), presumably because they feed less when spawning. Paterson (1968) however, noted no great difference between mature and immature lake trout, with respect to empty stomachs during the fall. There may be a seasonal decline in feeding activity for this species similar to that noted for pike by Johnson (1966) and for brown trout (Salmo trutta) by Swift (1961).

## Rainbow Trout

Rainbow trout were first introduced in the Medley River in 1963 and since that time approximately 5,000 fingerlings have been introduced there annually (K. Moller, pers. comm.). On one occasion yearlings were released and the 1972 introduction of coho salmon contained an unknown quantity of rainbow trout yearlings. No reproduction is known to have resulted from these plantings.

Two rainbow trout were netted in Cold Lake during the present study; one in 9 m of water in French Bay and one in 2 m of water near the Medley River, both specimens being (presumably) fish that had recently been introduced.

During their first summer in the Medley River rainbow trout eat a wide variety of terrestrial and aquatic invertebrate material. Specimens 30+cm fork length, weighing from 400-800 g, that had over-wintered successfully in the

Medley River, were examined during June and July of 1971 and 1972. Over 90% of the volume of food contained in their stomachs was ninespine sticklebacks. Individual trout contained up to 34 specimens consisting entirely of mature adults 4.9 + cm long of which over 66% were ripe females. The stomach containing 34 ninespine sticklebacks also contained a single adult brook stickleback. A shift to fish, where they are available, from an earlier diet of plankton and aquatic invertebrates is characteristic for rainbow trout (Scott and Crossman,1973) but cannibalism appears to be rare.

## The Distribution of Coho Salmon

Locality records for coho salmon are shown in figure 8. Netting results during the summer of 1970 and January-February of 1971 from Buchwald (1971) are shown in table 5. The catch per unit effort at depths less than 13.7 m was consistently higher than at greater depths, ranging from 1.67 - 2.58 salmon per 100 net-yard-night during the open water portion of the year. Nets set under the ice in January-February caught 0.43 salmon per 100 net-yard-night in shallow water and none in deep water. The results of simultaneous netting at depths greater or less than 13.7 m, during the summer of 1971 are shown in table 6. No salmon were taken at depths greater than 13.7 m, while 79 specimens were captured in water less than, or equal to

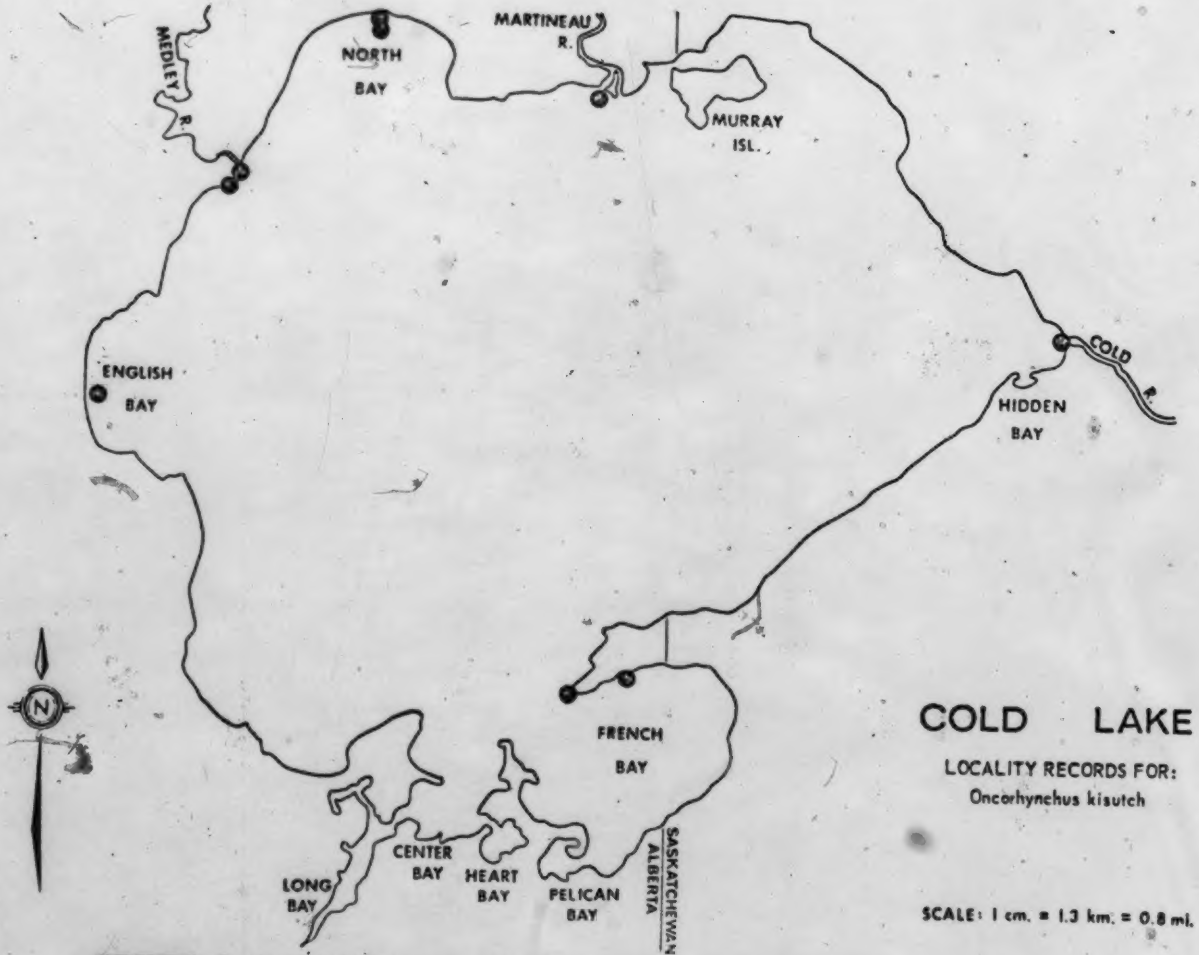

COLD LAKE
LOCALITY RECORDS FOR:
Oncorhynchus kisutch
SCALE: 1 cm. = 1.3 km. = 0.8 mi.
N
MEDLEY R.
NORTH BAY
MARTINEAU R.
MURRAY ISL.
ENGLISH BAY
COLD R.
HIDDEN BAY
FRENCH BAY
LONG BAY
CENTER BAY
HEART BAY
PELICAN BAY
SASKATCHEWAN
ALBERTA

FIGURE 8 Locality records for Oncorhynchus kisutch

Table 5. Gill-net catches of coho salmon in Cold Lake from July 1970 to February 1971.

| Month | Netting Effort (100 net-yard-nights) | Depth | No. of Salmon | No. of Salmon per 100 net-yard-night |
|---|---|---|---|---|
| July | 3.7 | <13.7 m. | 6 | 1.7 |
| | 5.2 | >13.7 m. | 2 | 0.4 |
| August | 0.6 | <13.7 m. | 0 | 0.0 |
| | 7.2 | >13.7 m. | 8 | 1.1 |
| November | 31.0 | <13.7 m. | 80 | 2.6 |
| | 3.0 | >13.7 m. | 4 | 1.3 |
| Jan.-Feb. | 23.0 | <13.7 m. | 10 | 0.4 |
| | 9.0 | >13.7 m. | 0 | 0.0 |

Table 6. Catches of coho salmon in simultaneous gill-net sets in water less than, and greater than 13.7 m.

| Month | <13.7 m | | >13.7 m | |
|---|---|---|---|---|
| | Netting Effort | No. of Salmon | Netting Effort | No. of Salmon |
| February | 1200 n-y-n | 0 | 1200 n-y-n | 9 |
| July | 250 n-y-n | 0 | 1300 n-y-n | 5 |
| August | 800 n-y-n | 0 | 2650 n-y-n | 45 |
| September | 650 n-y-n | 0 | 1400 n-y-n | 20 |

Table 7. Numbers of coho salmon taken at 1 m intervals from the surface in select depths of water during the summers of 1971 and 1972.

| Depth of water (m) | 0-3 | | | | 3-6 | | | | | | | 6-9 | | | | | | | | | | 9-13.7 | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Depth from surface (m) | 0 | 1 | 2 | 3 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13.7 |
| Number of specimens | 10 | 11 | 19 | 0 | 1 | 30 | 113 | 14 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 6 | 1 | 0 | 2 | 0 | 1 | 2 | 1 | 1 | 0 | 0 | 0 |

Table 8. Water temperatures at depth of capture and number of coho salmon captured at each temperature during August of 1972.

| Temperature °C | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of salmon captured | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 5 | 8 | 18 | 8 | 30 | 7 | 1 |

this depth. The catch per 100 net-yard-night in shallow water was 1.24 salmon. During 1972 all salmon netted were taken in less than 13.7 m of water, with the exception of those taken by commercial fishermen from water approximately 18 m deep, the depth of capture for which is uncertain. Salmon were taken by angling in shallow water and from the top 2 m of water about 10 m deep. The depths in the water column at which salmon were taken in water from 0 - 13.7 m deep is given in table 7. Most salmon were taken from water less than or equal to 6 m deep. In 1971-72, 89.1% of the salmon caught were taken in the upper 2 m of the water column. Ten of 18 specimens taken from water 9 - 13.7 m deep were caught in the upper 2 m. Salmon were rarely associated with the bottom at any depth of capture.

Table 8 shows the distribution of netted salmon in relation to water temperature at the depth of capture. Salmon were caught most frequently in 16° - 20°C water. Those taken at lower temperatures were, for the most part, in shallow water in late August, not from cooler water at greater depths.

## Discussion

Coho salmon in Cold Lake appear to occupy the surface waters close to shore and the upper portion of the water column in the shallow portions of bays. Coho salmon residuals (non-anadromous offspring of anadromous parents) in lakes such as Cultus Lake, B.C., occupy the shallow portions of the lake (Foerster and Ricker, 1952) while anadromous individuals tend to occupy the upper 3-4 m of the water column during the oceanic portion of their lives (Moiseev, 1956). Coho salmon introduced into inland lakes have distributed themselves variously in different lakes. In the Great Lakes they probably remain close to shore for the first few months before moving to the limnetic region (Scott and Crossman, 1973). A limnetic distribution was found for this species in Parvin Lake, Colorado, (Klein and Finnell, 1969) and in Pallette Lake, Wisconsin, (Engel, 1972). Klein and Finnell also found that inshore waters were occupied by coho salmon in Granby Reservoir, Colorado.

Engel (1972) attributed the increase in median depth at which coho salmon were taken, from May until August, to their avoidance of warm water. However his data indicate that there were not significantly more salmon taken at temperatures below 16°C than there were above this temperature. The temperatures with which coho salmon have been most frequently associated with during the summer, in other lakes where they have been introduced, range from 11.1°, in a Colorado reservoir (Korn and Smith, 1971) to 23.9°C in the shallows of Granby Reservoir, Colorado, (Klein and Finnell, 1969). Brett (1952) found that laboratory reared juvenile coho salmon avoided temperatures higher than 15°C and preferred temperatures of 12° - 14°C. Where temperature is the only parameter varied in a water column during preference experiments it may strongly influence the depth distribution of coho salmon, but the depth distribution and temperature associations of salmon in both native and introduced populations, especially the younger age classes, is not consistent with Bretts findings. Brett _et al_ (1958) concluded that the genus _Oncorhynchus_ was stenothermal but noted that the two characteristically piscivorous species, the coho and chinook salmon, could tolerate warmer water than the other species. It was also determined that the optimum temperature for sustained cruising, for coho salmon, was 20°C. The distribution of the members of a population may be expected to be concentrated at or near that portion of the habitat, within their range of temperature tolerance, where food is most readily available, and this may be more important in determining the distribution of coho salmon than their "preferred" temperature. This is further discussed with reference to the feeding of coho salmon (below). Alternatively the coho salmon may have occupied deeper, cooler waters, and made feeding excursions into the shallows and surface waters, during which, due to their increased activity, they were more susceptible to capture by gill-nets.

The maximum depth at which coho salmon were taken in Cold Lake was 36.6 m during the summer of 1970 (Buchwald, 1971). The occurrence of small salmon in deep water may be related to their migratory behavior, as migrating coho salmon smolts prefer deep water (Hoar, 1951). The migration of some members of the 1970 introduction (= 1969 stock) to lakes downstream from Cold Lake suggests that the lake was either not a suitable ocean substitute for these individuals, or that while it may not have been so for the stock as a whole only some individuals successfully located the outlet while their migratory drive was still sufficient to result in such downstream migration. Foerster and Ricker (1953) suggest that the occurrence of residual coho salmon in the last (downstream) lakes of river systems is owing to hereditary factors influencing migratory behavior.

An innate response enabling salmon smolts to successfully negotiate a lake during the course of their downstream migration would be selected for in populations where lakes are normally encountered by the smolts, and poorly developed or absent in populations that do not migrate through lakes. The existence of such hereditary factors has been demonstrated for sockeye salmon (O. nerka) by Groot (1965).

Based on netting results during the summers of 1971 and 1972, there is no evidence that the 1970 and 1971 stocks occupied deep water. It is uncertain whether the differences in depth distribution and migratory behavior was due to genetic differences, differences in the manner in which they were introduced, or a combination of these factors.

During 1972, monofilament nets placed across the Cold River outlet about 100 m downstream from the lake failed to catch any salmon from the 1971 stock leaving the lake, even though they were abundant immediately west of the outlet. During 1971, many individuals from the 1970 stock were netted at this location (west of the outlet). Buchwald (1971) concluded that a high portion of the 1970 stock was leaving the lake via the outlet but the river netting during 1972 indicated that the presence of coho salmon near the outlet was not necessarily associated with their leaving the lake. There were no reports of coho salmon from the 1970 and 1971 stocks being caught in the lakes downstream from Cold Lake as there had been for the 1969 stock. The presence of a current and its effects on the feeding of salmon (see below) may have resulted in the concentrations of this species near the outlet and at "Salmon Bay" near the Medley River, where catches were 0.94 and 1.06 coho salmon per 100 net-yard-night, compared with 0.64 and 0.5 coho salmon per 100 net-yard-night in the shallows of English and North Bays respectively.

Too few coho salmon of age class $2^+$ were taken to determine the distribution of this age class, however those taken were from shallow water, similar to that occupied by jacks and immature individuals. The relative paucity of older salmon may appear exaggerated if the older individuals differ in their distribution. However commercial fishing in deeper water with large mesh gill-nets yielded only a small number of immature individuals and no maturing individuals, other than precocious males, during July of 1972. The low numbers of $2^+$ salmon taken during each summer combined with low returns to the Medley River in the falls of 1971-1973 probably reflect low survival of coho salmon after their initial summer in Cold Lake.

## The Food of Coho Salmon

The food of coho salmon in Cold Lake was determined by analysis of the stomachs of 223 specimens collected during the open water seasons of 1971 and 1972. The diets of age class $1^+$ salmon from each year, and those of precocious males (jacks) and adult salmon are summarized in table 9 . Emerging and adult caddis flies dominated the diet of $1^+$ salmon during both years, accounting for 42.3 and 54.6 percent of the volumes eaten by this age class in 1971 and 1972, respectively. Ninespine sticklebacks constituted the second most important item and accounted for 14.6 % of the volume in 1971 and 24. % in 1972. Fish accounted for 17.2 % of the volume in 1971 and 33.9 % in 1972. Coregonid fishes, usually young of the year lake whitefish, ranked second as forage fish for $1^+$ salmon. Other fish eaten included juvenile walleye and suckers, and a single adult cyprinid. Terrestrial insects made up over 16% of the diet in both years. This group of food organisms was dominated by leaf hoppers (Hemiptera), Hymenoptera and Coleoptera. The remainder of the diet of $1^+$ salmon consisted of aquatic insects, Crustacea and leeches.

Ninespine sticklebacks comprised 56.9 % of the volume of the diet of precocious male salmon. Emerging and adult caddis flies ranked second in importance and constituted 17.9 % by volume of the diet. Coregonid fishes, again largely young of the year lake whitefish, ranked second in importance as forage fish. Leaf hoppers were the only

Table 9. Food items encountered in age class $1^+$ coho salmon of the 1970 and 1971 stocks, precocious males and adults.

| Food Item | $1^+$ (1970 stock) | | $1^+$ (1971 stock) | | Precocious males (1971 & 1972) | | Adults (1971 and 1972) | |
|---|---|---|---|---|---|---|---|---|
| | % Occurrence | % Volume | % Occurrence | % Volume | % Occurrence | % Volume | % Occurrence | % Volume |
| Trichoptera (adults) | 62.5 | 42.3 | 58.0 | 54.6 | 26.1 | 17.0 | 22.7 | 22.7 |
| Ninespine sticklebacks | 25.0 | 14.6 | 25.8 | 24.0 | 60.9 | 56.9 | 31.8 | 25.9 |
| Leaf hoppers | 25.0 | 5.1 | 12.9 | 13.2 | 8.7 | 8.6 | 4.5 | 1.8 |
| Lake whitefish | - | - | 3.3 | 3.3 | 8.7 | 8.7 | 9.1 | 7.7 |
| Cisco | 1.8 | 1.7 | - | - | 4.3 | 4.3 | 27.3 | 27.3 |
| Unidentified coregonids | 1.8 | 0.9 | 2.1 | 1.9 | 4.3 | 3.4 | 4.5 | 4.5 |
| Coleoptera | 30.4 | 8.1 | 1.1 | 0.1 | - | - | 13.6 | 9.1 |
| Hemiptera (Corixidae) | 12.5 | 6.2 | - | - | - | - | 9.1 | 7.7 |
| Diptera | 21.4 | 5.1 | 4.3 | 1.5 | - | - | 4.5 | 0.9 |
| Odonata | 23.2 | 8.3 | - | - | - | - | - | - |
| Hymenoptera | 28.6 | 5.4 | 2.1 | 1.2 | - | - | - | - |
| Ephemeroptera | 1.8 | 0.0 | - | - | - | - | - | - |
| Unid. insects | 8.9 | 1.6 | 2.1 | 2.3 | - | - | - | - |
| Amphipoda | 7.4 | 3.0 | - | - | - | - | - | - |
| Mysis | 1.8 | 1.1 | - | - | - | - | - | - |
| Hirudinea | 1.8 | 0.0 | 2.1 | 0.0 | - | - | - | - |
| Other fish | - | - | 3.2 | 2.7 | - | - | - | - |
| Unid. fish | - | - | 3.2 | 3.2 | - | - | - | - |
| No. of stomachs | 63 | | 98 | | 28 | | 30 | |
| No. with food | 56 | | 93 | | 24 | | 22 | |

terrestrial invertebrates encountered in jacks.

Fish comprised 57.7 % of the volume of the diet of adult salmon, consisting of 27.3 % cisco, 25.9% ninespine sticklebacks, and 4.5 % unidentified coregonids. Emerging and adult trichopterans were the most important invertebrates in the diet of adult salmon and made up 26.3% of the volume. Terrestrial insects (leaf hoppers) formed only 1.8 % of the diet, the remainder of which consisted of aquatic invertebrates other than caddis flies.

The food of age class $1^+$ salmon, including precocious males, is summarized to show the variation with length class in table 10. The volume of fish eaten increases with the size of the predator. Ninespine sticklebacks were eaten by salmon as small as 222 mm fork length.

Cisco were encountered singly or in twos in coho salmon stomachs while young of the year lake whitefish occurred singly, or up to three individuals per salmon stomach. Cisco removed from salmon stomachs were sub-adults or adults, and no young of the year individuals were found. Salmon preying upon cisco were as small as 365 mm (a precocious male).

All age classes of ninespine sticklebacks were encountered in salmon stomachs. Age class $1^+$ salmon preying on this species contained from 1-33 ($\bar{x}$ = 10.4) individuals during 1971, and from 1-100+ ($\bar{x}$ = 20.4) during 1972. Precocious male salmon preying upon ninespine sticklebacks contained from 1-110 ($\bar{x}$ = 27.7) individuals while the stomachs of seven adults

Table 10. Food items of age class $1^+$ coho salmon from Cold Lake showing variation by length classes during the summers of 1971 and 1972.

| Food Item | Length Class (mm)<br>150-199<br>% of vol. | 200-249<br>% of vol. | 250-299<br>% of vol. | 300-349<br>%of vol. | 350-399<br>% of vol. |
|---|---|---|---|---|---|
| Trichoptera (adults) | 100.0 | 59.2 | 45.2 | 0.0 | 11.0 |
| Leaf hoppers | - | 18.7 | 2.9 | 29.5 | - |
| Ninespine stickleback | - | 16.8 | 33.2 | 70.0 | 59.0 |
| Lake whitefish | - | 2.3 | 11.8 | - | 10.0 |
| Cisco | - | - | - | - | 20.0 |
| Unidentified coregonids | - | - | 3.9 | - | - |
| Diptera | - | 2.6 | - | - | - |
| Hymenoptera | - | 2.0 | - | - | - |
| Hirudinea | - | 0.6 | 0.0 | - | - |
| Unidentified fish | - | 0.5 | 2.8 | - | - |
| Walleye | - | - | 2.9 | - | - |
| Longnose sucker | - | 0.5 | - | - | - |
| Unidentified cyprinids | - | 0.5 | - | - | - |
| Total fish | - | 19.7 | 56.0 | 70.0 | 89.0 |
| Total invertebrates | 100.0 | 80.3 | 44.0 | 30.0 | 11.0 |

contained from 1-92 ($\bar{x} = 22.1$).

The frequency of empty stomachs in salmon of age class $1^+$ was 8.8% for the total number sampled during 1971 and 1972, exclusive of precocious males where 14.8% had empty stomachs. Only one adult salmon was found with no food in its stomach during June and July while many individuals taken near the river mouth in, or after late August, contained little or no food.

The winter food of coho salmon in Cold Lake is known from data presented by Buchwald (1971) based on analysis of 35 stomachs collected during late November of 1970 and February of 1971. Ten of the 26 specimens taken during November contained no food. The sixteen specimens containing food had eaten a total of nine Coregonus sp., one yellow perch, five unidentified fishes, one amphipod and one caddis fly. The eleven specimens collected in February contained one food item each; one yellow perch, three sticklebacks (Pungitius?) six unidentified fish and one aquatic beetle.

## Discussion

The food of coho salmon has been described for naturally occurring populations in fresh and salt water by numerous Asian and North American workers. Abramov (1949) reviewed the adaptive features and varying strategies of juvenile Oncorhynchus spp. including the coho salmon. The food of juvenile coho salmon in lakes has been documented by

Pravdin (1940), Ricker (1941), Gribanov (1948), Synkova (1951), Foerster and Ricker (1953), Roos (1960), and Mason (1974), while the food of juveniles in salt water is discussed in Piskunov (1955), Manzer (1969) and Parker (1971). The food of adults in salt water is documented in Silliman (1941), Pritchard and Tester (1944), Synkova (1951) and Prakash (1962).

The food of juveniles in introduced populations is described by Klein and Finnell (1969), Engel and Magnuson (1971), Engel (1972), Avery (1973) and Peck (1974). With the exception of Peck (1974) the former studies, along with Borgeson (1970) and Scott and Crossman (1973) discuss the food of "land locked" adult coho salmon.

The extensive use of aerial food, i.e. adult insects of aquatic or terrestrial origin, taken from the surface of the water, by juvenile coho salmon in Cold Lake, is consistent with the findings of others in both Asian and North American studies of natural populations, of this species and in investigations of introduced populations in North America. Norlin (1967) discusses the importance of terrestrial insects in the nutrition complex of lakes. While the biomass of these organisms is small compared to that of the benthic fauna, terrestrial insects on the surface of the water are concentrated in a single plane, frequently concentrated by the wind, readily seen from below and their ability to escape is hindered by their being entrapped by the surface tension of the water. When the winged adults of aquatic insects are found on the surface of the lake, they become more available to certain species of fish, such as the coho salmon, that are not specialized benthic feeders. Stomachs of coho salmon containing invertebrates taken from the surface of the water frequently contained, or were dominated by, a single type of prey, such as leaf hoppers or adult caddis flies. Where two such types of prey were encountered in a stomach, they were often segregated, with one type at the posterior end and the other at the anterior end of the stomach, with a well defined boundary where the two came into contact with each other. This probably reflects highly selective feeding by the coho salmon but may also be due to the temporary superabundance of these particular prey types. Different individuals captured at the same time and place appeared to be feeding selectively on different food types in some cases while on other occasions all specimens from a single sample preyed exclusively on a single food type. Selective feeding by coho salmon may be explained by the formation of a specific search image and may serve to increase the efficiency of the predator while preying upon a particular food type. Engel (1972) suggested that search image formation accounted for similar prey specialization by introduced coho salmon in Pallette Lake, Wisc. Individual specialization on a particular prey type has been noted for a number of species of the Salmonidae (Martin, 1952; Bryan and Larkin, 1972) and may result from differences of conditioned learning. While search image formation can result in intensive predation upon a particular prey type, differential food specialization may result in the reduction of intra-specific competition for a particular prey type, broaden the scope of the diet of the predator species at that time and place, and still maintain the advantages of selective feeding. "Indiscriminate" feeding as exhibited by some coho salmon may be viewed as being opportunistic and resulting from the low availability of any single prey type. It may well be adaptive where and when food is relatively scarce but the necessity for different search and capture techniques involved in this type of feeding probably result in it being less efficient than selective feeding under conditions of high abundance of prey.

Aerial food remains important during the open water season for all ages of coho salmon in Cold Lake although jacks and $2^+$ salmon appear to eat less than young salmon. The apparent increase in the use of aerial food by adult salmon when compared with its utilization by jacks may not be real. The number of salmon examined from these two classes is small and most of the adults sampled were taken during 1971 whereas the bulk of the jacks were caught during 1972. During 1972 caddis flies contributed more to the diet of young salmon than they did in 1971, perhaps due to differential availability during each of these years. Alternatively, other food types may have been more available during 1971, resulting in reduced predation upon caddis flies.

The contribution of fish to the diet of coho salmon increased with increasing size of the salmon. Fish did not enter the diet of young coho salmon in Cold Lake until mid-July, at which time the salmon were large enough to prey effectively upon ninespine stickleback adults or the young of the year whitefish that were moving into deeper water as they grew. Other species of forage fish did not appear to be abundant in the depths occupied by the coho salmon, most small species or recently hatched young of other species being found in one m of water along the lake margin. Coho salmon in natural populations in Kamchatka may shift to a partial diet of fingerling salmon at a size of 10-12 cm (Gribanov, 1948). Ricker (1941) and Roos (1960) observed that yearling coho salmon were important predators of sockeye salmon fry. Salmon of less than 20 cm probably experience difficulty in seizing and swallowing the ninespine stickleback adults because of the dorsal and pelvic spines of the sticklebacks. Observations of Salmo spp. preying upon brook sticklebacks in aquaria suggest that while it is physically possible for small salmonines to capture and swallow such spiny fish, it is accomplished with an inordinate expense of time and energy and accompanied by apparent discomfort. As the coho salmon grow, the spines of the prey become relatively smaller and are less of a deterrent to predation by larger salmon. Roos (1960) concluded that coho salmon preferred soft rayed fishes as prey. Threespine sticklebacks (Gasterosteus) were the most abundant small fish taken in seine hauls, but were absent from coho salmon stomachs in lakes near Chignik, Alaska. The spines of Gasterosteus are characteristically longer (in most populations studied), than those of ninespine and brook sticklebacks, and thus more likely to act as deterrents to predation by small coho salmon. Gasterosteus is eaten in large quantities by age class $2^+$ coho salmon in a closed, relict, Kamchatka Lake (Gribanov, 1948). The size of coho salmon may be important in determining whether or not spiny-rayed fish are included in the diet.

Size does not appear to be the only factor involved in determining the time at which fish enter the diet of coho salmon. It is apparent from the studies of Gribanov (1948) and Abramov (1949) that there is no characteristic size at which a change from feeding on invertebrates to fish occurs. Perhaps the availability of appropriate forage fish is an important factor, for where salmon fry are encountered as they emerge from their redds, they dominate the diet of yearling coho salmon (Synkova, 1951).

Toward the end of July, large aggregations of young of the year ninespine sticklebacks which occasionally include one or more adults, may be seen in shallow water up to at least three m deep. These aggregations appear to represent a readily available source of food for the yearling (and older) coho salmon. Grinols and Gill (1968) describe the manner in which coho salmon successfully attack schooling fishes. Coho salmon charge into the aggregated prey, seizing some and dispersing the aggregation. Following this they circle the prey as the aggregation is reformed and then they charge again. Schools of lake whitefish and cisco are probably preyed upon in a similar fashion, the former species as the young of the year lake whitefish move into deeper water and the latter when they are found inshore and near the surface in late summer and fall. Many of the fish species eaten by coho salmon, in the ocean and in freshwater lakes to which they have been introduced, are frequently found in schools. While attacking schools of fish requires a great deal of energy, it can result in a greater return over a period of time to the predator that can do so successfully, than a less active mode of predation by the same, or another predator. The ability of this species to consume and assimilate large quantities of forage fish, results in rapid growth. Larger salmon are faster swimmers and their larger mouths permit them to feed on a broader range of prey items. In Cold Lake this is manifest by the inclusion of sub-adult and adult cisco in the diet of large jacks and age class $2^+$ individuals. Predation by coho salmon upon cisco may be restricted to those portions of the year when the surface waters and shallow regions are cool enough to permit breakdown of the apparent mid-summer partial segregation of these two species in Cold Lake. Large $2^+$ salmon may move out into the limnetic region and prey more extensively on cisco than the data suggest. However evidence for this is lacking.

The frequency of empty stomachs during the summer, for non-maturing individuals, and maturing individuals prior to their return to the Medley River, is low and probably indicative of a high rate of active feeding. The percentages of stomachs containing food during the summer in the studies of Engel (1972) and Peck (1974) were 97% and 95% respectively. Prakash (1962) reported the number of coho salmon containing food in southern B.C. coastal waters averaged over 90% during the summer months. The frequency of empty stomachs in Cold Lake increased as the gonads matured during and after late August, as is characteristic for natural populations of this species (Gribanov, 1948; Prakash, 1962). The intensity of feeding by non-maturing individuals decreases during the winter (Gribanov, 1948; Synkova, 1951, Avery, 1973) at which time the percentage of stomachs containing food is low, as is the fullness of the stomachs containing food.

During the winter, there is a marked decrease in the consumption of food by coho salmon in Cold Lake. The specimens containing food averaged only one item per stomach. Owing to the low temperature of the water and the consequent slow rate of digestion of food these items may have been in the stomach for a number of days. The low rate of consumption of food by coho salmon during the winter may be due to the reduced ability of this species to capture prey. Brett et al (1958) found that juvenile coho salmon had a sustained cruising speed of less than 10 cm/sec at 0°C, while at 20°C they cruised from 30-45 cm/sec. While the low winter water temperatures in Cold Lake probably affect all species of fish present in a similar manner, the extent of the effects may be greater on southern species near the northern limits of their range or on exotics that normally do not encounter such low temperatures. Keast (1968) found that certain species of fish were unable to maintain their body weight during the winter due to reduced consumption of food. From the growth data for coho salmon in Cold Lake (Buchwald, 1971; Moller, 1972) it appears that there is no gain in the weight of these fish between November and June. Coho salmon in Pallette Lake, Wisconsin, exhibited only a slight gain in weight for one age class during one winter, while in other years, this introduction and other introductions of the same species lost weight between October and April. Predation upon coho salmon by native piscivores, notably the northern pike may be at a maximum during this period, due to the reduced ability of the salmon to escape. One pike from a small number netted near the Martineau River during the winter contained a coho salmon of age class $1^+$. The occurrence of coho salmon in the stomachs of northern pike from the lake proper is slightly less than one per hundred examined. However when the number of pike in Cold Lake is considered along with the number of times each consumes food during one year it becomes apparent that they probably represent an important predator of coho salmon.

## The Distribution of Northern Pike

Locality records for northern pike in Cold Lake are shown in figure 9. The numbers of pike and catch per unit effort at selected depths are shown in table 11. Young of the year individuals were not seen or collected except at the mouth of the Medley River and age class $1^+$ individuals were uncommon in net catches. The maximum depth at which northern pike were taken was 24 m. This species ranked fourth in numbers of fish taken in gill-nets during this study and accounted for 5.2% of the number of fish caught.

## Discussion

The northern pike appears to be widespread in the littoral region of Cold Lake throughout the open water season. It is less abundant in areas of North, English and other sandy bays where rooted aquatic vegetation is scarce, and absent from the pelagic region in the middle of the lake. Rawson (1951) found that 90% of the northern pike gill-netted in Great Slave Lake were taken within 1/4 mile of the shore. The vertical distribution of this species is restricted when compared to those of the other native piscivores but is consistent with the generalizations of McPhail and Lindsey (1970) and Scott and Crossman (1973) that the northern pike is an inhabitant of shallow lakes or shallow bays within deeper lakes, although its maximum depth is given at over 30 m in the latter account. From table 11 it can be seen that more

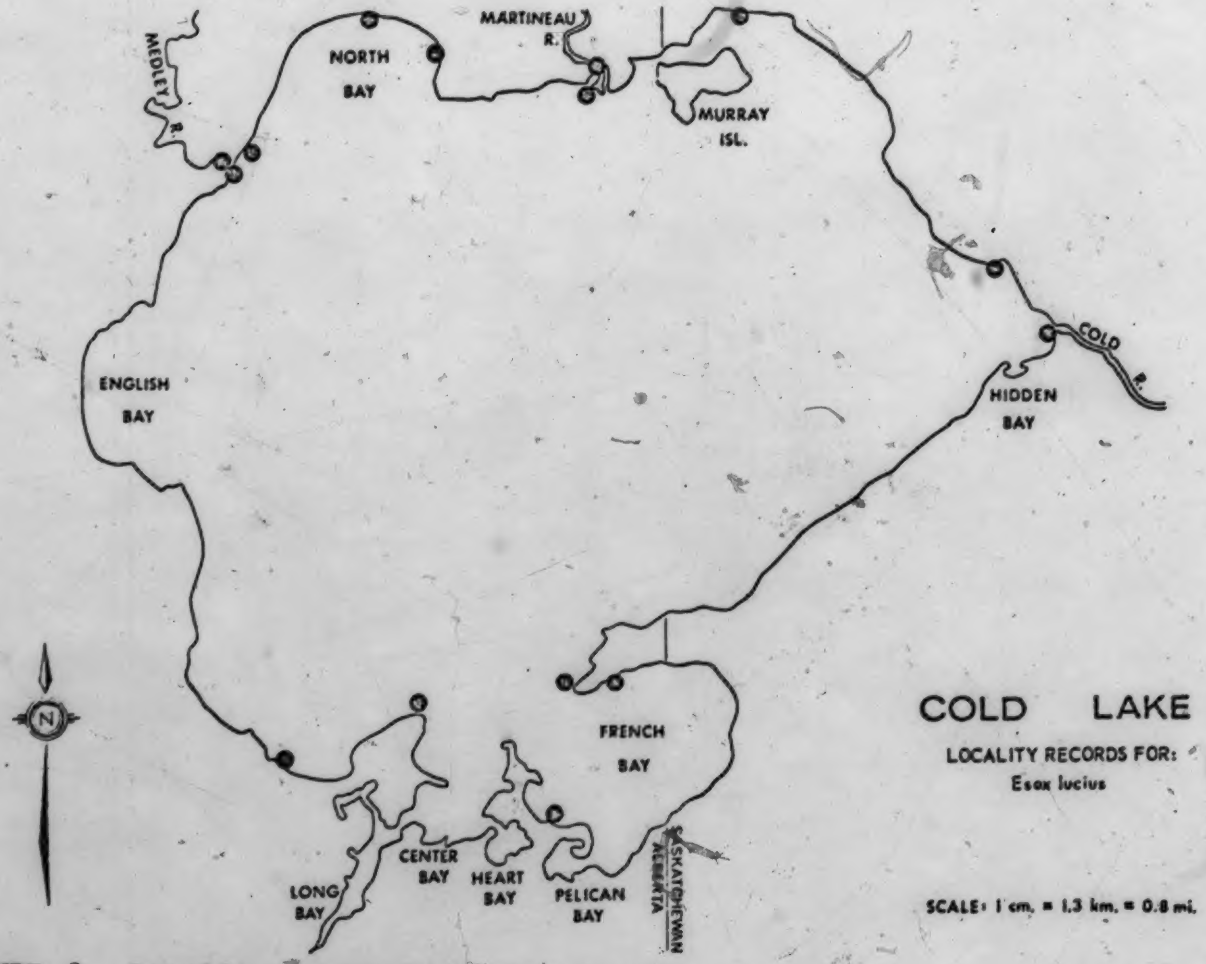

MEDLEY R.
NORTH BAY
MARTINEAU R.
MURRAY ISL.
ENGLISH BAY
COLD R.
HIDDEN BAY
N
FRENCH BAY
LONG BAY
CENTER BAY
HEART BAY
PELICAN BAY
SASKATCHEWAN
ALBERTA
COLD LAKE
LOCALITY RECORDS FOR:
Esox lucius
SCALE: 1 cm. = 1.3 km. = 0.8 mi.

FIGURE 9 Locality records for Esox lucius

Table 11. Catches of northern pike in selected depths of water from May to August of 1972. No./100 net-yard-night in parentheses.

| Depth in m | May | June | July | August |
|---|---|---|---|---|
| 6 | 40 (40) | 58 (1.17) | 148 (3.44) | 103 (2.34) |
| 9 | - | 7 (1.75) | - | 12 ( .75) |
| <13.7 | - | 11 (1.83) | 43 (4.52) | 2 (2 ) |
| >13.7 | - | 52* (17.3) | 5 ( .76) | 6 ( .5 ) |

* 39 Specimens taken in one set (100 n-y-n) in Long Bay.

fish per unit effort are taken in water less than 13.7 m than in greater depths throughout most of the lake. Exceptionally, when catches in French and Long Bays are compared with those from similar depths in other parts of the lake northern pike are more abundant in these two bays than in other parts of the lake at all depths down to 15.2 m. It appears from gill-net catches and returns to anglers that the population of pike is higher in these areas than in other areas of similar depth. Within these bays large areas of habitat suitable for spawning are found, and aside from that available in tributaries, this accounts for most of the spawning habitat within the lake proper. Adults congregate in these areas in the spring, possibly moving considerable distances within the lake to get there. Following spawning, dispersal away from the shallows, and perhaps for many individuals away from these bays would appear necessary as a means of reducing intraspecific competition for food and space. Similarly the young age groups reared in these areas must disperse to some extent. Makowecki (1973) found from tagging recoveries that aside from spawning time, the movement of adults was limited and that they might even be considered territorial. Young northern pike in aquaria tend to be spaced at discrete distances, possibly as a result of intraspecific competition (Frost and Kipling, 1967). Congregation of adults in spawning areas, followed by gradual dispersal of some individuals, including newly recruited ones, away from these areas probably gives rise to the high density of northern pike in the bays adjacent to spawning and rearing habitat.

Ripe adults also enter the tributaries shown in figure 8 or possibly utilize what little vegetation they can find along the lake margin, for spawning. All specimens taken on and after May 10, 1972, were spent.

Young age classes, up to age $2^+$ appear to be most common in the areas where the adults spawn although some age $2^+$ individuals are taken in the lake proper. Small fish and cover are both abundant in the areas where pike spawn. The lack of small pike from areas along the lake shore with abundant forage fish but no vegetation suggests that vegetation is important for the survival of small northern pike. The partial segregation of young from older age classes may serve to reduce cannibalism within this species.

## The Food of Northern Pike

The food of northern pike in Cold Lake was determined from observations of stomach contents of specimens sampled in 1971, from analysis of 225 pike stomachs taken from May to September of 1972 and an additional 24 specimens taken in September of 1974. The diet of northern pike in Cold Lake is summarized in table 12. The major items in terms of percentage occurrence in those stomachs containing food were: ninespine sticklebacks (71.0%); slimy sculpins (20.3%);

Table 12. Stomach contents of 225 northern pike from Cold Lake, May to September of 1972.

| Food item | Percent occurrence[a] | Percent of volume |
|---|---|---|
| Ninespine stickleback | 71.0 | 58.8 |
| Slimy sculpin | 20.3 | 15.0 |
| Cisco | 7.2 | 6.6 |
| Hirudinea | 7.9 | 5.7 |
| Burbot | 3.6 | 3.6 |
| Yellow perch | 2.2 | 2.2 |
| Coho salmon | 2.9 | 2.0 |
| Northern pike | 1.4 | 1.4 |
| Insects | 1.4 | 1.4 |
| Suckers | 2.9 | 1.3 |
| Lake whitefish | 0.7 | 0.7 |
| Unid. salmonoid | 1.4 | 0.7 |
| Unid. fish | 2.9 | 0.7 |
| Walleye | 0.7 | 0.4 |
| Amphipods | 0.7 | 0.4 |
| Fish eggs | 1.4 | 0.2 |
| Spottail shiner | 0.7 | 0.2 |
| Lake chub | 0.7 | 0.7 |
| Fathead minnow | 0.7 | 0.1 |
| Empty (no, and % of 225) | (87) 38.7 | |

[a] percent occurrence in stomachs containing food.

leeches (7.9%); cisco (7.2%); and burbot (3.6%). Food items other than vertebrates occurred in 10.7% of stomachs containing food.

Table 13 lists items occurring as exclusive food in northern pike stomachs, their percentage occurrence as exclusive food items and the mean number of each prey item per predator containing that particular prey item. 81.1% of the northern pike with food in their stomachs contained only a single "species" of food, while 18.8% contained a combination of food items. 38.6% of the stomachs examined contained no food. Ninespine sticklebacks were the exclusive food of 49.2% of the northern pike containing food. The average number of ninespine sticklebacks per stomach was 8.1, slightly more when they were the exclusive contents of a stomach and slightly less when they were found in combination with other food items. All other species of fish eaten by northern pike occurred most frequently as single individuals, whether they were the exclusive prey or in combination with other food items. Slimy sculpins were the only fish other than ninespine sticklebacks that commonly occurred in numbers greater than one, up to an observed maximum of nine per predator stomach. Burbot were found to occur only as single individuals and were always the exclusive food of the northern pike in which they occurred. Leeches were the exclusive food of 60% of the northern pike in which they were found and occurred singly or in twos.

Table 13. Items occurring as the exclusive food in individual pike, their percentage occurrence as exclusive food and mean numbers of each per stomach in which they occur.

| Food item | % occurrence as exclusive food | Number of individuals per stomach | | |
|---|---|---|---|---|
| | | minimum | mean | maximum |
| ninespine stickleback | 49.3 | 1 | 8.1 | 35 |
| slimy sculpin | 9.4 | 1 | 1.9 | 9 |
| cisco | 4.3 | 1 | 1.2 | 3 |
| Hirudinea | 4.3 | 1 | 1.6 | 2 |
| burbot | 3.6 | 1 | 1 | 1 |
| yellow perch | 1.4 | 1 | 1 | 1 |
| coho salmon | 2.2 | 1 | 1 | 2 |
| northern pike | 1.4 | 1 | 1 | 1 |
| insects | 1.4 | 1 | 1 | 1 |
| suckers | 0.7 | 1 | 1.7 | 4 |
| lake whitefish | 0.7 | 1 | 1 | 1 |
| lake chub | 0.7 | 1 | 1 | 1 |
| Total | 81.1 | | | |

The seasonal change in the diet of northern pike is shown in table 14. Ninespine sticklebacks were the most important food item throughout the summer, while slimy sculpins increased in importance from early to late summer. Coho salmon were most frequently found in northern pike in June. Young northern pike were found in the stomachs of adults only during the month of May.

Predation upon ninespine sticklebacks is documented for the months of June, July and August of 1972 in table 15. The mean number of individuals per predator stomach is at a maximum in June and decreases during each successive month. Ripe female sticklebacks outnumbered males 146-44 removed from northern pike stomachs.

Table 16 shows the size and numbers of northern pike eating ninespine sticklebacks, salmonids, and ~~burbot~~, along with the mean number of each prey item per predator containing it. The 70 cm length class of northern pike contained the highest average number of ninespine sticklebacks per predator. Larger northern pike (80 and 90 cm length classes) contained fewer ninespine sticklebacks and some were found to prey upon burbot.

## Discussion

Due to its allegedly enormous appetite the food and feeding of the northern pike has been the object of numerous studies. These studies have included examination

Table 14. Seasonal change in the diet of northern pike in Cold Lake. (Principal prey items only, percentage occurence).

| Food item | June | July | August |
|---|---|---|---|
| ninespine stickleback | 56.1 | 62.3 | 51.8 |
| slimy sculpin | 5.3 | 18.0 | 27.8 |
| cisco | 5.3 | 8.2 | 3.7 |
| Hirudinea | 7.0 | 1.6 | 9.2 |
| burbot | 3.5 | 1.6 | 3.7 |
| coho salmon | 5.3 | - | - |
| no. of food types (scope of diet) | 14 | 12 | 8 |
| stomachs examined | 80 | 89 | 77 |
| empty and % empty ( ) | 23 (28.7) | 28 (31.5) | 23 (29.9) |

Table 15. Seasonal change in the consumption of ninespine sticklebacks by northern pike in Cold Lake, June-August, 1972.

| | June | July | Aug. |
|---|---|---|---|
| No. of northern pike containing ninespine sticklebacks | 32 | 38 | 28 |
| Total number of ninespine sticklebacks consumed | 285 | 246 | 158 |
| $\bar{X}$ no./stomach as exclusive prey | 13.9 | 8.6 | 5.1 |
| $\bar{X}$ no./stomach (mixed and exclusive | 12.4 | 7.2 | 5.6 |

Table 16. The food of northern pike showing variation by length classes.

| Predator size (10 cm length classes) | Number of northern pike containing each prey species. No. in parentheses indicates mean no. of prey items per predator. | | | | |
|---|---|---|---|---|---|
| | Ninespine sticklebacks | Lake white-fish | Cisco | Burbot | Coho Salmon |
| 40-49.9 | 1 | - - | - - | - - | 1 (1) |
| 50-59.9 | 11 (11.8) | - - | - - | - - | 1 (1) |
| 60-69.9 | 12 (18.7) | 1 (1) | 3 (1.6) | - - | - - |
| 70-79.9 | 8 ( 8.6) | 1 (1) | - - | 3 (1) | - - |
| 80-89.9 | - - | - - | - - | 2 (1) | - - |

of the relationship between producer and consumer and the role of predators in fisheries (Frost, 1954; Johnson, 1966; Popova, 1967), the role of northern pike in the life cycles of parasites such as Triaenophorus crassus (Miller, 1943; Lawler, 1965) and the potential of this species as a control to prevent overcrowding and stunting in panfish populations (Johnson, 1969). Northern pike have been utilized in studies of the effectiveness of spines as defensive structures and their role in influencing and prey selection of predators (Hoogland et al, 1957; Beyerle and Williams, 1968). Nursall (1973) examined the relationship between a schooling cyprinid, the spottail shiner, and two of its predators, the pack-hunting yellow perch and the solitary northern pike.

The diet of northern pike in the present study, and in previous studies suggest that they are opportunistic predators. While they appear to be opportunistic there is evidence that they may also be somewhat selective in their feeding. They were found to avoid threespine sticklebacks (Gasterosteus aculeatus) after they had experienced them where alternate (non spiny) prey was available (Hoogland et al. 1957), and selected non spiny fish when offered a choice between sunfish (Centrarchidae) and minnows (Cyprinidae) (Beyerle and Williams, 1968). The relatively short spines of ninespine sticklebacks do not appear to deter northern pike in Cold Lake. Hoogland et al (1957) noted that the shorter spines of ninespine sticklebacks compared to those of threespine sticklebacks were not as effective in deterring predation by northern pike as were those of threespine sticklebacks. Their experiments were also conducted utilizing small predators and it was realized that larger individuals might not be similarly deterred. Frost (1954) found that northern pike longer than 40 cm ate more threespine sticklebacks than they did minnows even though the latter were more abundant. The chain pickerel (Esox niger) was found to prey upon young bullheads (Ictaluridae) even though they were the least common species of forage fish in Lincoln Pond, New York (Raney, 1942). It appears that small spines are not effective deterrents, from the point of view of preventing predation upon those species that possess them, against large northern pike and its congeners.

Size selection of prey items by northern pike appears evident from the results of previous studies (Frost, 1954; Lawler, 1965; Popova, 1967; Beyerle and Williams, 1968; Johnson, 1969; Makowecki, 1973), in which studies larger pike tended to utilize larger prey items (when size was determined by measuring their respective lengths). Hoogland et al (1957) suggested that the shift noted in Frost's study, from a diet dominated by minnows to one dominated by threespine sticklebacks with increasing predator size was due to a corresponding increase in the optimum size of the prey. The increase in predation upon threespine sticklebacks with increasing predator size was evident among length classes up to and including

50 cm, but dropped off in larger fish, again perhaps as a result of shift in optimum prey size. Lawler (1965) found that the numbers of small yellow perch in northern pike increased to a maximum value in individuals slightly over 35 cm and then decreased. The numbers of spottail shiners and trout-perch eaten increased with increasing predator size to maxima of approximately 45 and 50 cm for northern pike preying on these species respectively. Such shifts are perhaps manifest in the diet of northern pike in Cold Lake where predation upon ninespine sticklebacks increases with increasing predator size and reaches a maximum in the 60 cm size class after which the mean number of individuals per predator stomach declines. The few northern pike in excess of 70 cm and containing food most frequently contained food items in excess of 20 cm, in which cases there is a great increase in the length of the prey item relative to that of the predator.

Johnson (1969) concluded that the relationship between length of predator and length of prey was less important than that for jaw width of the predator and maximum depth of the prey. Ninety-three percent of the northern pike he examined contained prey items, the maximum depth of which were less than the jaw width of the predator; 3.6% contained prey equal to the predator jaw width and only 2.7% contained prey with a body depth greater than the jaw width of the predator. The relationship of the prey depth to the jaw width of the predator, combined with the spiny first dorsal fin of sunfish may account for the rejection of large individuals seized by northern pike in the experiments of Beyerle and Williams (1968). While body depth of prey items may render the prey difficult, if not impossible, for predators to swallow, body length alone offers little protection against predation by northern pike, for they are occasionally found with relatively long prey protruding beyond their jaws (Johnson, 1969; personal observations), the prey being slowly swallowed as digestion permitted. With the exception of adult yellow perch and walleye, all of the species of fish present in Cold Lake appear to have a body form that is readily swallowed by northern pike, yet those occurring in stomachs are, in most cases, much smaller than the maximum size that the predator is able to swallow.

The dominant item in the diet of northern pike in Cold Lake, the ninespine stickleback, is probably the most abundant and readily available forage fish throughout most of those portions of the study area inhabited by pike. Large (4.5 - 6.5 cm) ninespine sticklebacks, particularly ripe females, were preyed upon disproportionately with respect to their abundance within the species, while young of the year and year old individuals were rarely eaten. Forage fish from one to three cm long may provide a smaller net return to the predator in terms of energy expended during their capture. It is also possible that large northern pike are poorly adapted as predators of extremely small fish.

While they are abundant, small whitefish and cisco are infrequently included in the diet of northern pike in Cold Lake. This is consistent with the findings of Lawler (1965), who noted that coregonines were only occasionally eaten by small (30 cm) individuals, and Makowecki (1973) who noted that only 6.5% of the lake whitefish found in northern pike stomachs were less than 35 cm long. There were six and seven alternative prey species utilized by northern pike in the two lakes studied by Lawler (1965) and Makowecki (1973). Perhaps solitary prey such as slimy sculpins and ninespine sticklebacks, and aggregated prey such as breeding ninespine sticklebacks are more readily preyed upon by northern pike than are similar sized, schooling coregonines. Nursall (1973) concluded after observing northern pike attack schooling fish, that a school of fish is "not an exceptionally attractive target for the pike". Mauck and Coble (1973) found that in spite of it occurring in schools, the gizzard shad (Dorosoma cepedianum), was the species most vulnerable to predation by northern pike among those utilized in their study, but this herbivorous species is perhaps relatively sluggish, its best defense appearing to be its deep body and rapid growth. Raney (1942) suggested the disproportionate predation by chain pickerel on young catfish was due to the ease with which they were captured. This may have contributed to the disproportionate utilization of threespine sticklebacks observed by Frost (1954), and may, in combination with their abundance account for the importance of ninespine sticklebacks and slimy sculpins in the diet of northern pike in Cold Lake.

The increase in the frequency with which slimy sculpins are encountered in northern pike stomachs in mid and late summer may be due to changes in the behavior and microhabitat distribution of this forage fish. Slimy sculpins are most vulnerable to predation when they are actively foraging and moving around, especially when they are found in rocky areas. All individuals (with one exception) removed from northern pike stomachs were mature adults. During their breeding season male slimy sculpins guard the eggs deposited by females under rocks or other suitable cover and are thus less likely to be eaten by northern pike. While females might not enjoy the same protection, numerous breeding ninespine sticklebacks are encountered in the same areas and are preyed upon extensively which may serve to reduce the predation pressure on slimy sculpins, and indeed on other forage fishes.

Two of fourteen post-spawning pike examined near a spawning area in May of 1972 contained one yearling pike each. Throughout the study area yearling pike appear to be rare, thus minimizing the opportunity for cannibalism among the members of this species.

Coho salmon were eaten by northern pike in the lower reaches of the Medley River in June when the smolts were present in large schools as they were moving or preparing to move from the river into Cold Lake. Only one other coho salmon was found in a pike stomach during the remainder of the summer. A single specimen was also taken from a pike caught near the Martineau River during the winter of 1971-72.

The intensity of predation as measured by the average number of ninespine sticklebacks per meal may be taken as an index of feeding activity as they are at all times the most important diet item and are relatively constant in terms of per cent occurrence. Feeding activity appears to be at a maximum in June, decreasing during each successive month. Johnson (1966) found that feeding intensity in northern pike reached a peak in June and decreased throughout the summer. A similar June peak in activity followed by a decline was observed in semi-captive northern pike in Kakisa Lake, N.W.T. (D. Christiansen, pers. comm.). Lawler (1965) and Johnson (1969) suggested that feeding intensity decreases during the summer on the basis of a high percentage of empty stomachs encountered at that time, however the interpretation of the significance of empty stomachs requires careful consideration.

An empty stomach merely indicates that a period of time, during which digestion has taken place, has elapsed since the organism ingested its last meal. It is most important to know when the organism ate last, the duration of the digestive process, and when, if ever, the organism will eat again. With an understanding of these events more accurate conclusions can be drawn with respect to the consumption of food of an organism over a period of time.

While experimental data concerning these events in northern pike are lacking, an hypothesis can be generated to explain the conflicting conclusions with respect to feeding intensity, drawn by Johnson (1966) and Lawler (1965). During the summer, empty stomachs encountered in northern pike in Cold Lake were generally flaccid, which indicates that the fish had recently ingested and digested a meal. This is in contrast with the condition of the stomachs observed in fasting, pre-spawning salmon, and the centrarchid fishes examined by Keast (1968) that had apparently not fed for some time, the stomachs of which were shrunken and drawn far forward in the body cavity. There appears to be a lag period, following digestion of a meal by northern pike, that precedes ingestion of the next meal. The digestion rate for northern pike at various temperatures ranges from one day at 20 C to nine days at 0 C (Popova 1967). If the lag period is one day, at 20 C the percentage of empty stomachs would be close to 50% because, for the feeding "cycle" described, a fish that had eaten and digested food during one day would be in its lag phase the following day. At lower temperatures, assuming that the lag phase is of the same duration, since the rate of digestion is slower, the number of stomachs containing food will be higher. Assuming that the meal size at different temperatures is constant, the amount of food consumed over a given period of time will be greatest at high temperatures even though the frequency of empty stomachs is also greatest at that time (see table 17). The figures presented in table 17 represent the results expected if the feeding sequence of ingestion, digestion, and post feeding lag is adhered to strictly, and that constancy of meal size and duration of lag phase is maintained at all temperatures. Individual variations with respect to feeding sequence and length of lag phase, along with seasonal variation of these and meal size will almost certainly alter the figures in table 18, but if these variations are not large, they will merely dampen or exaggerate the trends expressed and not obliterate them. From this table it can be seen that during the summer at high temperatures the consumption of forage fish may, as Johnson (1966) observed, have been at a maximum, yet the frequency of empty stomachs provides "evidence" for a reduction in the intensity of feeding during this period, as was concluded by Lawler (1965) and Johnson (1969). Further study is required to determine the duration of the lag phase and its variability, both individual and seasonal.

Lawler (1965) and Johnson (1969) reported no differences in the feeding of male and female northern pike. When the sexual dimorphism with respect to size is considered

Table 17. Food consumption and frequency of empty stomachs at different temperatures by northern pike[a]:

| Digestion Rate (Days)[b] | Frequency of Empty Stomachs (per cent) | Consumption of Food[c] | Temperature (°C) |
|---|---|---|---|
| 1 | 50 | 3.5 | 20 |
| 2 | 33 | 2.7 | 14-15 |
| 3 | 25 | 1.7 | - |
| 9 | 10 | 0.7 | 0 |

[a] Hypothetical (strict feeding schedule assumed and only the digestion rate changing with temperature change).

[b] From Popva (1967)

[c] Relative quantities per unit time.

however a qualitative difference in the food of male and female pike becomes apparent. The largest male pike taken during this study was 715 mm fork length and all other males were less than 700 mm. Individuals in excess of 700 mm eat fewer ninespine sticklebacks than do smaller northern pike, and include a different, larger species of prey, the burbot.

## Cyprinidae-Distribution and Life History Notes

In terms of number of species present, Cyprinidae is the best represented family of fishes in Cold Lake. The seven species occurring in Cold Lake do not appear to be widespread or abundant. Locality records for these species are shown in figures 10 and 11.

The spottail shiner appears to be very abundant locally, large schools being encountered near the mouth of the Medley River and near the dock at the town of Cold Lake. Seining in other areas yielded few specimens and unlike some of the other species of fish they were seldom observed. Aggregations observed from the town dock resembled those described by Nursall and Pinsent (1969) in Beaver Lake, Alberta, in that they were associated with juvenile yellow perch, but differing in the occasional inclusion of lake chub and ninespine sticklebacks. Many species of fish were taken simultaneously in seine hauls at the mouth of the Medley River but due to the tea-colored water it was impossible to observe any associations that might have existed

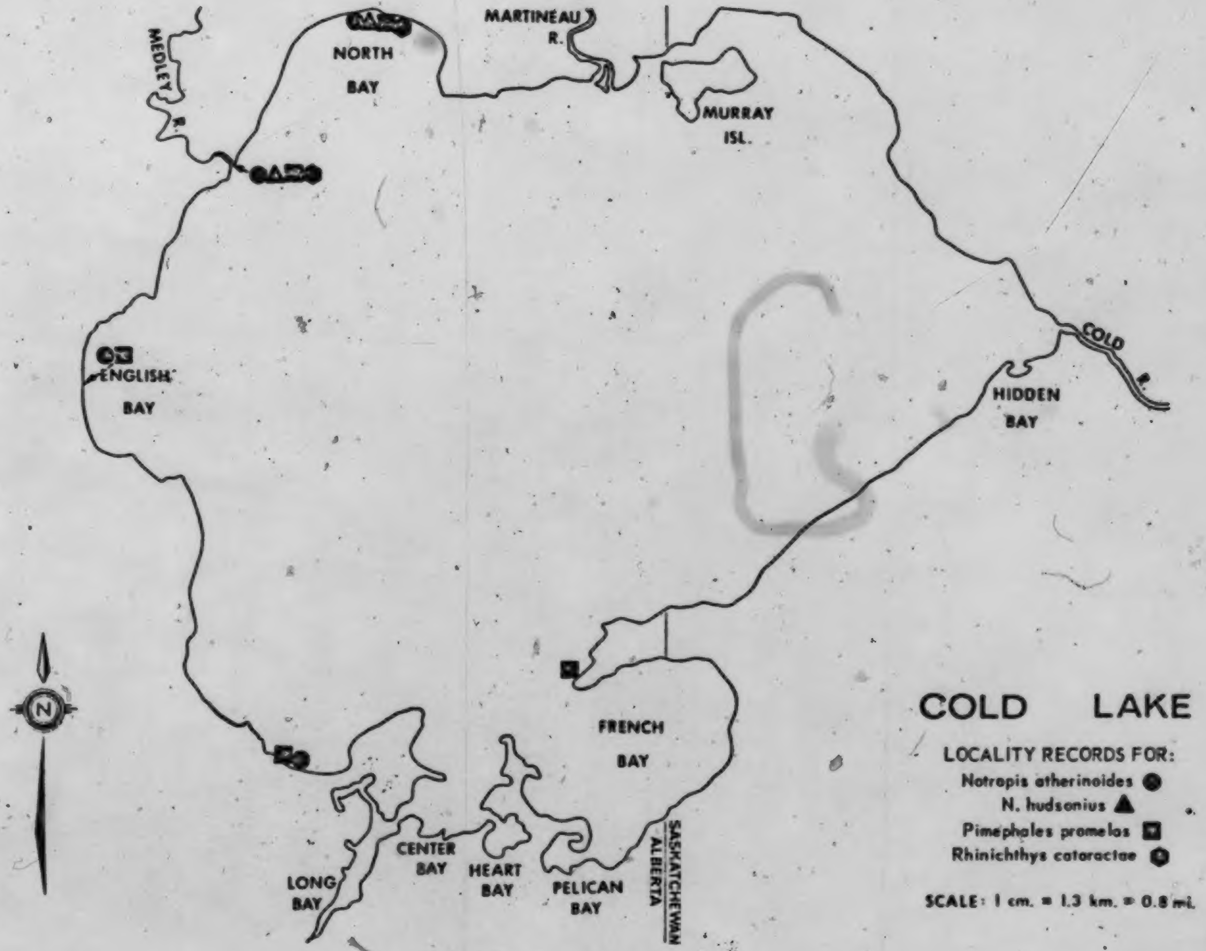

MEDLEY R.
NORTH BAY
MARTINEAU R.
MURRAY ISL.
ENGLISH BAY
COLD R.
HIDDEN BAY
FRENCH BAY
LONG BAY
CENTER BAY
HEART BAY
PELICAN BAY
SASKATCHEWAN
ALBERTA
N
COLD LAKE
LOCALITY RECORDS FOR:
Notropis atherinoides ●
N. hudsonius ▲
Pimephales promelas ▣
Rhinichthys cataractae ⬢
SCALE: 1 cm. = 1.3 km. = 0.8 mi.

Figure 10 Locality records for four species of cyprinid fishes

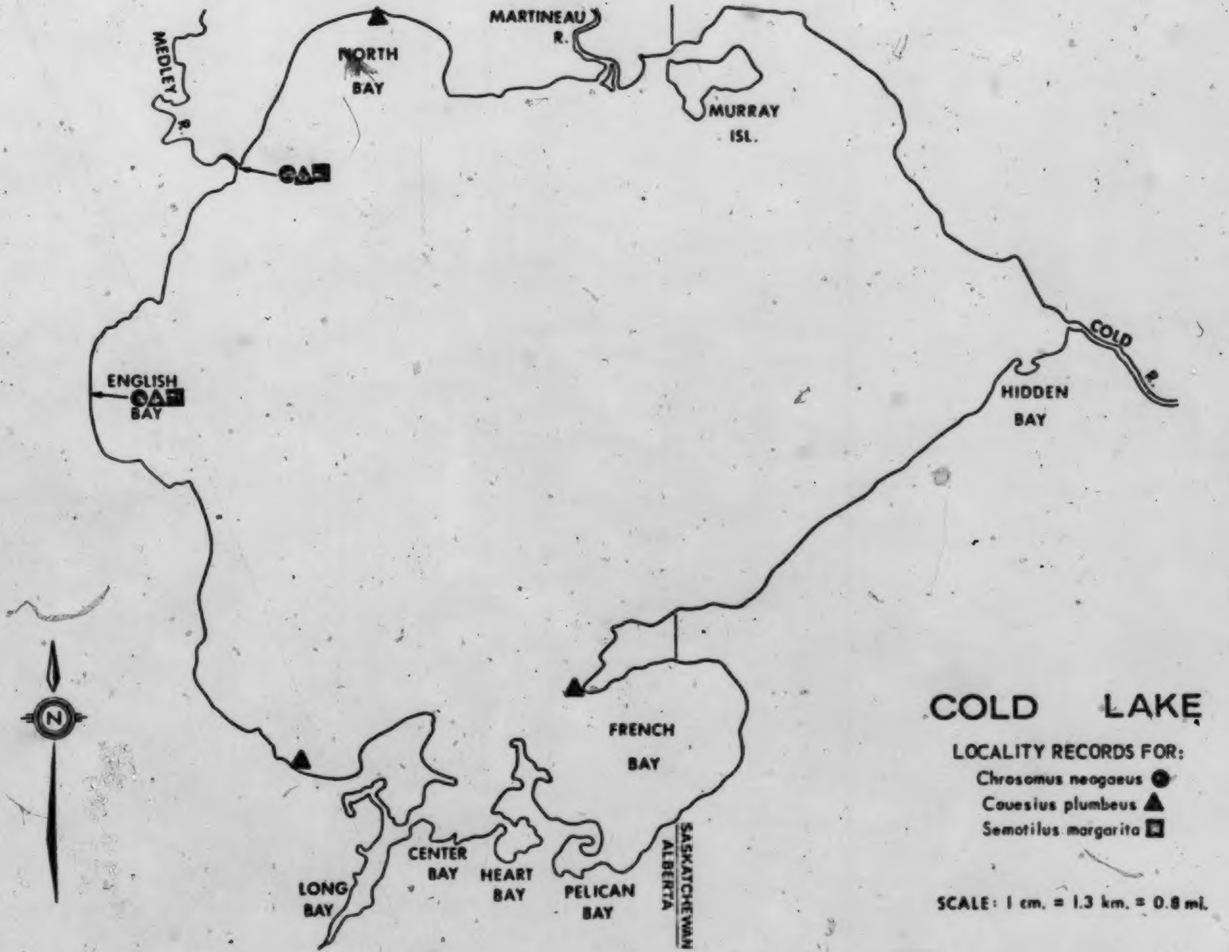

MEDLEY R.
NORTH BAY
MARTINEAU R.
MURRAY ISL.
ENGLISH BAY
COLD R.
HIDDEN BAY
FRENCH BAY
LONG BAY
CENTER BAY
HEART BAY
PELICAN BAY
SASKATCHEWAN
ALBERTA
N
COLD LAKE
LOCALITY RECORDS FOR:
Chrosomus neogaeus ●
Couesius plumbeus ▲
Semotilus margarita ▣
SCALE: 1 cm. = 1.3 km. = 0.8 mi.

Figure 11 Locality records for three species of cyprinid fishes

there. Spottail shiners are often the most abundant cyprinids in northern lakes (Scott and Crossman, 1973), where in large lakes such as Great Slave Lake, they are found in the shallows (McPhail and Lindsey, 1970). In the Great Lakes this species prefers the shallowest waters (Wells and House, 1974), generally occurring at depths of seven fathoms (12.6 m) or less. Spottail shiners prey selectively upon zooplankters and aquatic insects (McCann, 1959; Smith and Kramer, 1964). During and immediately following their breeding period in early summer, large individuals were found to prey upon their own eggs and larvae. McPhail and Lindsey (1970) state that spottail shiners occasionally small fish but do not elaborate. Large individuals examined throughout the summer in Cold Lake contained invertebrates only.

The emerald shiner was infrequently collected along the shore in North Bay and the mouth of the Medley River. This species is pelagic and schools offshore, often near the surface, in the summer (Scott and Crossman, 1973). This species is subject to wide fluctuations in numbers and Fuchs (1967) documented high male mortality after their first year of life. Whether the scarcity of this species is real or merely apparent is not known for Cold Lake. The diet of emerald shiners includes microcrustacea, midge larvae and some algae (Fuchs, 1967).

The lake chub is perhaps the most widespread cyprinid

The adults have relatively small swim bladders compared with their young, resulting in their being less buoyant, and adapted for benthic life (Gee and Northcote, 1963). Where the substrate permits it, longnose dace forage between and under the rocks, where they also spend a great deal of time when they are inactive. Such behavior probably renders this species less susceptible to both predation by other fish and seining. Adults feed on the most abundant and available benthic invertebrates (Gerald, 1966).

The fathead minnow was collected most frequently in the Medley River, its lagoon and mouth, but was occasionally taken along the lake margin in seines. A single specimen was taken in a minnow trap near Garnet Beach, from 3 m of water, where another specimen was obtained from a northern pike stomach. The rocky areas along the lake margin could provide suitable breeding habitat for this species however breeding individuals were not observed there. Algae form an important portion of the diet in Ohio (Coyle, in Scott and Crossman, 1973). Organic detritus, chironomid larvae and zooplankton were eaten by specimens from northern Alberta (McPhail and Lindsey 1970).

The finescale dace was first noted in Cold Lake in 1971 from collections made in and near the Medley River mouth. It was common in the river but not found far from its mouth in the lake. Additional specimens were collected in the temporary stream flowing from a small lake to the west of Cold Lake into English Bay. These specimens (University of Alberta Museum of Zoology=UAMZ catalogue numbers 3308, 3309) constitute the first records of this species from the Churchill River drainage in Canada and were reported by Roberts (1973). These records support the contention of McPhail and Lindsey (1970) that the lack of records from this area might be due to lack of intensive collecting in suitable habitats. Few stomachs of this species have been examined but its chief food appears to be insects, crustacea and zooplankton being less frequently encountered (McPhail and Lindsey, 1970; Scott and Crossman, 1973).

## Catostomidae-Distribution and Life History Notes

Locality records for longnose and white suckers are shown in figure 12. Both species were encountered at most locations but not always simultaneously. Longnose suckers were most commonly taken in nets at depths from 3-13 m and encountered at a maximum depth of 24.6 m. Most adults taken from less than 3 m were caught near the Cold River which differs from most of the shallow areas of the lake in that it has a strong current and frequently lower temperature. While this species is widespread and abundant in the northern portion of its range it is less abundant and confined to the deeper areas of lakes in the south (Scott and Crossman, 1973). During the summer it has been associated with temperatures of 11-11.6°C in Moosehead Lake, Maine, while white suckers were found to be associated with

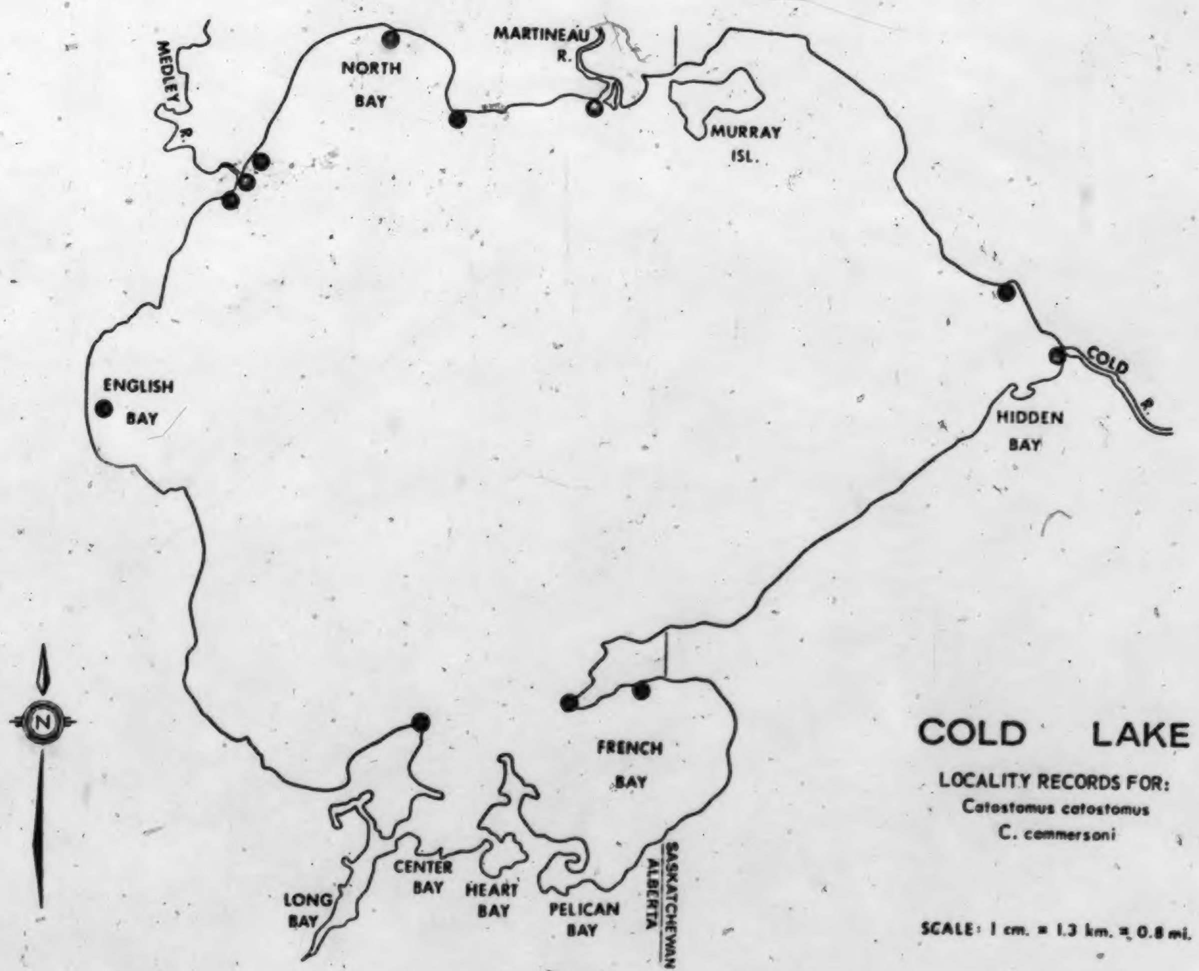

COLD LAKE
LOCALITY RECORDS FOR:
Catostomus catostomus
C. commersoni
SCALE: 1 cm. = 1.3 km. = 0.8 mi.
MEDLEY R.
NORTH BAY
MARTINEAU R.
MURRAY ISL.
COLD R.
HIDDEN BAY
ENGLISH BAY
FRENCH BAY
LONG BAY
CENTER BAY
HEART BAY
PELICAN BAY
SASKATCHEWAN
ALBERTA
N

Figure 12 Locality records for Catostomus spp.

temperatures from 14.1-18.3°C (Ferguson, 1958). Longnose suckers have been taken from depths as great as 180 m in Lake Superior (Scott and Crossman, 1973). In Cold Lake white suckers were most commonly taken in 4 m of water but were taken as deep as 37 m. This species is usually found in the top 6-10 m of lakes but has been taken below 47 m in Great Slave Lake (Scott and Crossman, 1973). During the study sub-adults of both species were most commonly taken in 3 m or less while those recorded at the maximum depth for each species were mature adults. Large numbers of adults of both species entered the Medley, and presumably the Martineau Rivers in late April and early May for the purpose of spawning. Longnose suckers preceded white suckers into the Medley River, however in mid-May, there appeared to be spawning activity of longnose suckers along the sand bars along the river mouth.

Young of the year suckers were abundant near the Medley River mouth in late June at which time they were 15-25 mm long. At Waskesieu Lake, Saskatchewan, the fry of white and longnose suckers migrate to the lake from their natal stream from one to two weeks after hatching (Scott and Crossman, 1973). At this time white suckers are 10-12 mm long and longnose suckers from 12-17 mm long. Clifford (1972) found that most downstream movement of white sucker larvae in the Bigoray River, Alberta, occurred at night, and suggested that it was the result of active swimming. Young of the year suckers became densely distributed around the lake margin within 2 m of the shore and in water less than 0.5 m along sandy beaches or in water 1 m deep along rocky shores. As the summer progressed and the fry grew larger they moved further from shore and were found in schools. Occasionally schools of age $1^+$ suckers were observed along the shore but they were probably characteristic of slightly deeper water.

Suckers were exceeded in net catches by cisco and whitefish only and accounted for 7.3% of the catch during the 1971 netting program of this study. White suckers were more abundant than longnose accounting for 6.4% of the catch. Young of the year suckers were the most abundant small fish taken in seines along the lake margin.

The stomachs of adults of both species of suckers were examined and found to contain exclusively invertebrates. There have been no reports of predation on vertebrates (other than fish eggs) by suckers. Suckers may be important predators of fish eggs in Cold Lake, especially those of the native salmonids because they are not protected by a redd. Scott and Crossman (1973) review the evidence for suckers as egg predators and conclude that they appear to be overrated in this respect. Atkinson (1931) reported predation by white suckers upon lake trout eggs, but Martin (1957) did not consider them to be a serious fish egg predator. Paterson (1968) found that while other fish, including lake trout, ate lake trout eggs in Swan Lake, Alberta, nine white suckers taken at the same time contained none. White suckers have been cited as important predators of logperch eggs (Ellis and Roe, 1917). During lake whitefish spawning time, the stomachs of 100 white suckers from individuals caught on a spawning bed, contained no eggs (Campbell, 1935).

Young of the year suckers were observed to feed at or near the surface, and in mid-water, until late in their first summer when they fed largely upon benthic material. This change can be attributed to the ontogeny of the mouth, which, in newly hatched individuals is terminal in position. By the time the young sucker has attained a length of 16-18 mm the mouth becomes inferior. Mid-water and surface feeding persists in individuals in excess of 20 mm, perhaps owing to the abundance of plankton available and the incomplete development of the inferior mouth.

Adult suckers were not noted from the stomachs of any piscivorous fish during the present study. Northern pike are said to take adult longnose suckers (Scott and Crossman, 1973) and Lawler (1965) found that large pike in Heming Lake ate large white suckers. Adult catostomids are frequently eaten by large pike in the Red Deer River (personal observations). In Cold Lake only young of the year and age class $1^+$ suckers were eaten by other fish and only for the young of the year walleye were they a major food item. They may form an important part of the diet of young of the year pike in the Medley River or other pike rearing areas.

## The Distribution of Burbot

Locality records for burbot in Cold Lake are shown in figure 13. The catch per unit effort at select depths throughout the summer is shown in table 18. Catches of burbot decreased in the shallow waters as the summer progressed. Net catches indicate that the distribution of this species is clumped. Burbot were taken at a maximum depth of 97.5 m at which point they appeared to be abundant. Young of the year were not collected.

## Discussion

With the exception of water less than 3 m deep burbot were present in all areas of the lake sampled. While young of the year may be active in shallow water in daylight, older individuals tend to seek cover and are quiescent during the daytime (personal observations). In rivers burbot tend to occupy the maximum depth possible (Malinin, 1971). Burbot are active at night or under low light intensities, with the exception of mid-summer (Muller, 1973) and it may be that older burbot are sensitive to high light intensities. The decrease in catches of burbot in shallow water may be due to reduced activity in late summer, however burbot may still be taken in deep water, and a seasonal change in depth distribution may occur. In southern and central Canadian lakes butbot are restricted to the hypolimnion during the summer and have been taken at depths of 212 m (Scott and Crossman,

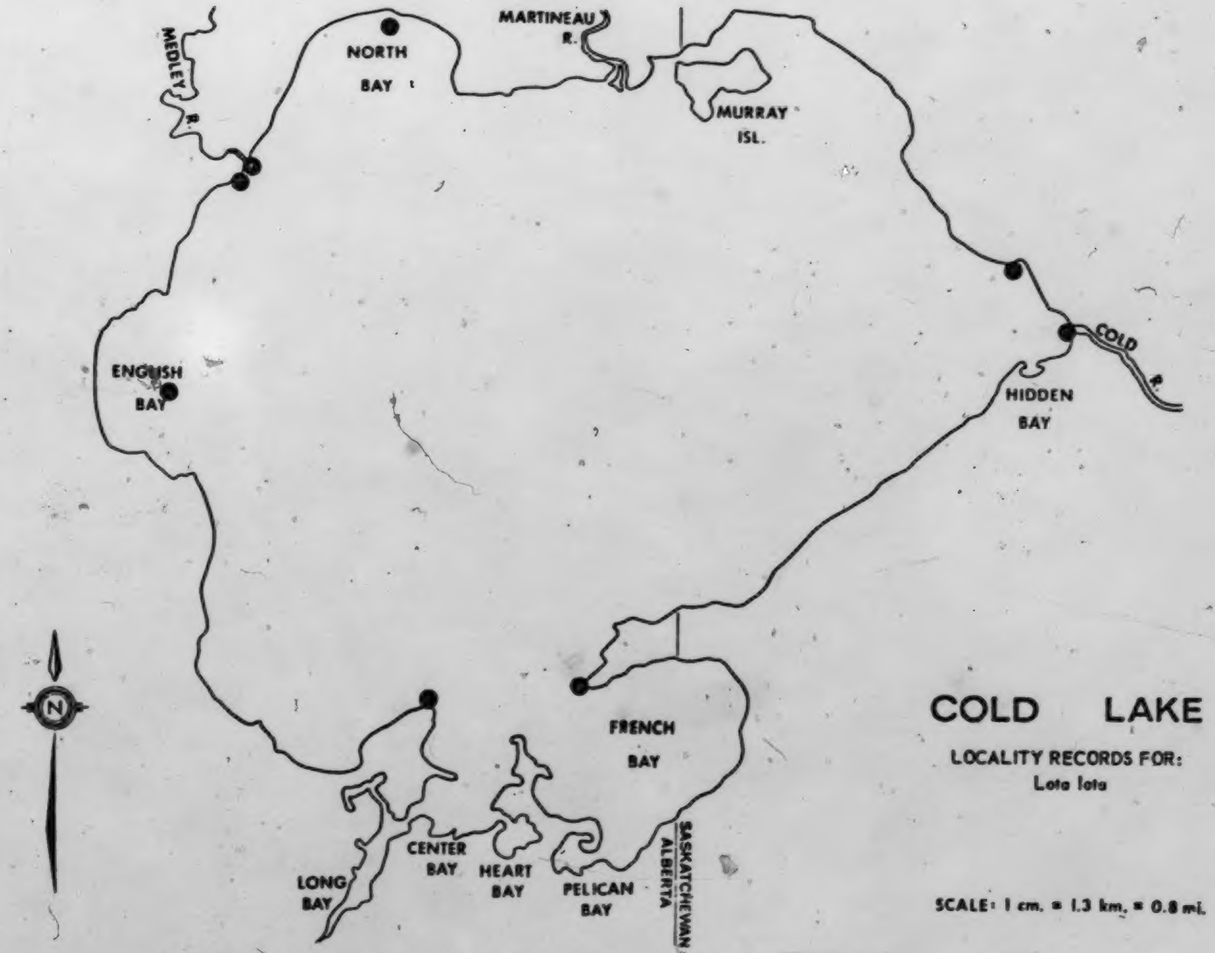

COLD LAKE
LOCALITY RECORDS FOR:
Lota lota
SCALE: 1 cm. = 1.3 km. = 0.8 mi.
N
NORTH BAY
MARTINEAU R.
MURRAY ISL.
MEDLEY R.
ENGLISH BAY
COLD R.
HIDDEN BAY
FRENCH BAY
SASKATCHEWAN
ALBERTA
PELICAN BAY
HEART BAY
CENTER BAY
LONG BAY

Figure 13 Locality records for Lota lota

Table 18. Burbot catches in depths up to 30.48 m (100') July-October, 1955[a].

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Mean depth of set (m) | 3.04 | 7.61 | 10.6 | 13.7 | 16.1 | 19.8 | 22.8 | 29.9 | 28.9 |
| Number of burbot | 0 | 0 | 10 | 37 | 25 | 25 | 12 | 2 | 2 |

[a] from Miller (1956).

1973), but may move into the shallows at night. Burbot in Moosehead Lake, Maine, were associated with temperatures from 10.8 - 11.4°C (Ferguson, 1958). These temperatures approximate those at which Miller (1956) obtained maximum catches of burbot in Cold Lake at depths from 13.7 - 20 m. Miller found that while burbot were taken in the deepest sets, they were far less abundant below 25.9 m. That burbot appeared to be abundant in the deepest set, 97.5 m, during the present study may be due to their distribution being clumped. At a given depth some sets contained few or no burbot while others contained large numbers. Level, sandy-bottomed areas yielded the smallest catches while rocky-bottomed areas and drop-offs yielded the largest.

Miller's catches were made with 5-1/2" stretched mesh gill-nets and averaged 1.84 kg while most nets used during the present study were smaller and the average size of burbot was less than 500 g. If no changes in the growth rate or age class structure are assumed, then the results of netting will be biased in favor of smaller burbot, the distribution of which may differ from that of larger individuals. This appears to be so for the young of the year in other lakes, where they frequent shallow sandy areas. The distribution of this age class in Cold Lake is uncertain, but they may be associated with rocky substrate along the bottom and margin of the lake making their capture by both predators and ichthyologists difficult.

## The Food of Burbot

### Results

The stomach contents of 29 burbot are listed in table 19. Fish were found in less than half of the stomachs containing food. In most cases these consisted exclusively of ninespine sticklebacks. Seven of eleven burbot stomachs from individuals taken in shallow water contained fish while amphipods dominated the diet of individuals taken in deep water. Approximately half of the burbot examined contained two or more classes of food simultaneously. Large burbot contained larger numbers of ninespine sticklebacks than did small ones but all sizes of burbot contained prey items from within a common size range.

### Discussion

These data combined with observations from the summer of 1971 indicate that fish are less frequently utilized for food by burbot in Cold Lake than in other bodies of water. Fish is the chief food of the burbot in Great Slave Lake (Rawson,1951) and in Heming Lake, Manitoba, where aquatic invertebrates were found occasionally but only in small individuals up to a length of 38.1 cm (Lawler,1963). The diet of small burbot, up to 500 mm long, consists of invertebrates for the most part with fish being uncommon, while for burbot over 500 mm long, fish is almost the exclusive food (Scott and Crossman,1973). Few burbot in

Table 19. The stomach contents of 26 burbot from Cold Lake.

| *Pontoporeia* | *Gammarus* | *Hyallela* | *Mysis* | Gastropoda | Hirudinea | Fish eggs | Cisco | Ninespine stickleback | Brook stickleback | Unidentified fish remains | Size of burbot (fork = total length) in cm |
|---|---|---|---|---|---|---|---|---|---|---|---|
| X | - | - | - | - | - | - | - | - | - | - | 28-39.9 |
| X | - | - | - | - | - | - | - | - | - | - | " |
| X | - | - | - | - | - | - | - | - | - | - | " |
| X | - | - | - | - | - | - | - | - | - | - | " |
| X | - | - | - | - | - | - | - | - | - | - | " |
| X | - | - | - | - | - | - | - | - | - | - | " |
| X | - | - | - | - | - | - | - | - | - | - | " |
| X | - | - | - | - | X | - | - | - | - | - | " |
| - | X | X | - | - | X | - | - | - | - | - | " |
| X | - | - | - | - | - | - | - | 5 | - | - | " |
| X | - | - | - | - | - | - | - | 1 | - | - | " |
| X | - | - | X | - | - | - | 1 | 1 | - | - | " |
| - | - | - | - | - | - | X | - | 2 | - | - | " |
| - | - | - | - | - | - | X | - | 4 | - | - | " |
| X | - | - | - | - | - | X | - | - | - | - | " |
| - | - | - | - | X | X | X | - | 1 | - | - | " |
| - | - | - | - | - | - | X | - | 2(+) | - | - | >40 |
| - | - | - | - | - | - | - | - | 17 | - | - | " |
| - | - | - | - | - | - | - | - | 8 | - | - | " |
| - | X | - | - | - | - | - | - | - | - | - | " |
| - | - | - | - | - | - | - | - | 2 | 1 | - | " |
| - | - | - | - | - | - | - | - | 8 | - | - | " |
| X | - | - | - | - | - | - | - | 9 | - | X | " |
| X | - | - | - | - | - | - | - | 8 | - | - | Unknown |
| - | - | - | - | - | - | - | - | 2 | - | - | " |
| - | - | - | - | - | - | - | - | 1 | - | - | " |

excess of 500 mm were examined during the present study, and most specimens were 400 mm or less in length. Although the sample size is small it appears evident from table 20 that more of the individuals in excess of 400 mm contained fish than did smaller burbot. The high incidence of Pontoporeia in the diet of smaller burbot in Cold Lake may be due to the availability of this species due to its abundance and the paucity of cover, combined with the limited availability of sufficiently small forage fish on the bottom in the deeper waters frequented by burbot.

Lawler (1963) found that of 15 species of fish present in Heming Lake, only 8 species were preyed upon by burbot, and of these, only 3 species constituted more than 2% of the fish ingested. During the summer, yellow perch, trout-perch, and ninespine sticklebacks, in decreasing order of importance, were the dominant diet items of burbot, while northern pike and white suckers which were very abundant, were seldom eaten. Lawler suggested that the burbot is most effective preying upon active swarming fishes, and thus the solitary, less active nature of the pike would render it less susceptible to predation by burbot. Suckers were thought "not to be a preferred food type". It was concluded that burbot appear to prefer some types of forage fish to others regardless of abundance. Another interpretation is possible.

The apparent selective predation upon certain forage species by burbot may be a product of the distribution and behavior of the predator and their relationships to those of potential forage fish. "Burbot evidently feed at night", (McPhail and Lindsey 1970) and there is a noticeable increase in their activity following sunset (Malinin 1971). Burbot catches by anglers "still-fishing" increase during and after the onset of darkness (personal observations). Malinin (1971) demonstrated that olfaction and detection of vibrations by means of lateral line receptors enable the burbot to hunt successfully in complete darkness. In cases where potential prey species are quiescent at night, olfaction would appear to be important for locating prey, and lateral line detection for "homing in" on prey produced vibrations resulting from their normal activity or perhaps excitation elicited by the presence of the approaching predator. Emery (1973) found that fish, in general, were more easily approached at night than in the daytime. Such quiescent behavior in yellow perch has been suggested as a means of escaping detection by predators that rely on vibrations, in part, for locating their prey (Hasler and Villemonte 1953). While such behavior on the part of yellow perch (and indeed other forage fishes) might provide protection from certain predators such as the northern pike, it may render them more susceptible to predation by burbot. The three species of fish most frequently encountered in burbot stomachs by Lawler (1963) are known to rest on the bottom at night (Emery, 1973). Trout-perch and yellow perch do this in the areas they occupy during the day, while ninespine sticklebacks rest on the bottom after they move into deeper water at night (Emery, 1973). In Cold Lake the ninespine stickleback appears to be the only species from this group that occupies areas frequented by burbot. Small cisco might be expected to occupy areas where they would encounter burbot but Emery (1973) noted that their behavior at night was highly variable and included activity, inactivity and occupation of various portions of the water column. Some elements of this variable behavior may have survival value with respect to predation by burbot and indeed might be an adaptive response to such predation. Cisco were found to be the most frequently utilized forage fish for burbot in Great Slave Lake (Rawson, 1952) where they were the most abundant "large" fish and constituted 46% of the fish netted in the depth range where burbot were most common. A single cisco was found in a burbot taken from deep water in Cold Lake during the summer and further specimens were encountered in the stomachs of burbot taken during the winter when both species are found in shallow water. Other forage fish frequently eaten by burbot in Great Slave Lake were also very abundant at the depths where burbot were found.

Young of the year northern pike and white suckers and small sub-adults of these species are found in shallow water in Cold Lake where they are not subject to predation by burbot and similar ecological separation of burbot and these species in Heming Lake may account for their minor role in the diet of burbot there.

The single brook stickleback found in a burbot stomach represents the only record of this species in the diet of a fish in Cold Lake.

The burbot may be an important predator of fish eggs in Cold Lake. Five burbot contained the eggs of either ninespine sticklebacks or slimy sculpins. Burbot are known to eat large quantities of cisco eggs (Scott and Crossman, 1973).

Burbot are generally regarded as voracious carnivores and have been noted to contain up to 179 fish in a single individual (McPhail and Lindsey, 1970; Scott and Crossman, 1973). Lawler (1963) stated that burbot stomachs containing from 80-100 trout perch or ninespine sticklebacks were not uncommon. The maximum number of fish noted in a burbot stomach from Cold Lake was 17, while the mean number was 5.1. The low mean value is probably due, in part, to the small size of the burbot examined, and that they frequently contained other types of food along with fish.

### Brook Stickleback

Brook sticklebacks were collected at only four sites during the present study (see figure 14). Collections generally consisted of one or two specimens, the only exception to this being a large number entangled in Chara sp. which was, itself, entangled in a gill-net dragged across the bottom near the Cold River.

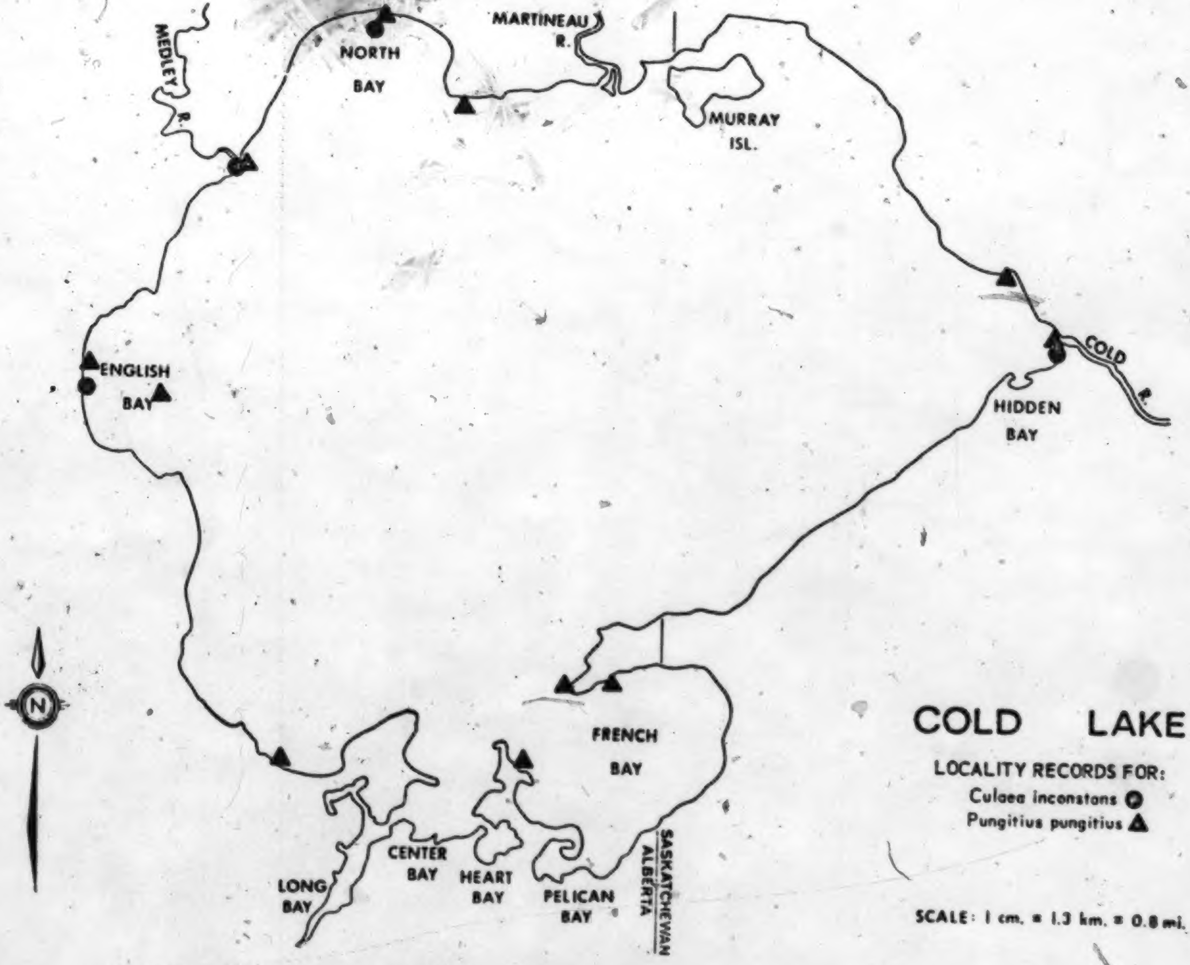

COLD LAKE
LOCALITY RECORDS FOR:
Culaea inconstans ●
Pungitius pungitius ▲
SCALE: 1 cm. = 1.3 km. = 0.8 mi.
MEDLEY R.
NORTH BAY
MARTINEAU R.
MURRAY ISL.
COLD R.
HIDDEN BAY
ENGLISH BAY
FRENCH BAY
SASKATCHEWAN
ALBERTA
LONG BAY
CENTER BAY
HEART BAY
PELICAN BAY
N

Figure 14 Locality records for Culaea and Pungitius

Scott and Crossman (1973) describe the usual habitat of this species as densely vegetated areas in flowing water and swampy margins of beach ponds of larger lakes. Such habitat is not characteristic of the greater part of Cold Lake, occurring only at the locations indicated in figure 14, three of which are tributaries and their mouths. The numerous specimens collected near the Cold River may have originated from the outlet stream or the shallow weedy bay southwest of it, indicated in figure 14. Brook sticklebacks may be more abundant in the shallow weedy portions of Long and French Bays, and the Martineau River mouth and weedy shoreline adjacent to it.

The diet of brook sticklebacks in Astotin Lake, Alberta, was studied by Robinson (1972) who noted that this species is almost completely carnivorous, preying largely upon chironomid larvae, cyclopoid nauplii, amphipods and ostracods. Cannibalism occurred but was rare. Scott and Crossman (1973) note that the eggs and larvae of other fishes are eaten by brook sticklebacks. At the time of Robinson's study, Astotin Lake was populated largely, if not exclusively, by a single species of fish, thus the role of the larvae of other species of fish in the diet of brook sticklebacks may be greater than indicated in his results.

Predation on brook sticklebacks by other fish was noted only twice during the present study, once in the lake proper by a burbot and once in the lower reaches of the

Medley River by a rainbow trout that contained a single adult individual along with 34 adult ninespine sticklebacks. Brook sticklebacks are preyed upon by a number of species of piscivorous fish but probably not as a preferred food item (Scott and Crossman 1973). Lawler (1965) found that they formed a small portion of the diet of northern pike in Heming Lake, Manitoba, while Makowecki (1973) found that in Seibert Lake, Alberta, brook sticklebacks ranked second as a forage fish for the same predator, occurring in 8.7% of those containing food and averaging 9 specimens per stomach. Brown trout are occasionally found to be gorged with brook sticklebacks in small streams such as Mud Creek, tributary to the Clearwater River (personal observations). Brook sticklebacks might be expected to provide forage for rainbow trout in the Medley River, especially during the period from August-April, when ninespine sticklebacks are not commonly found there. Due to the apparently limited occurrence of brook sticklebacks within the lake proper, its role as both a piscivore and a forage fish would seem minimal.

## Ninespine Stickleback

Ninespine sticklebacks were collected or observed at nearly all points sampled along the lake margin throughout the open water season with the exception of the month of August. The June-July distribution of this species is shown in figure 14. Scattered individuals were observed or collected at many locations along the lake margin in May as soon as open water was encountered. During June and July dense aggregations were present along the lake margin within depths of 0.5 - 5 m, and within the Medley River upstream as far as the culvert under the Primrose highway. These aggregations consisted almost exclusively of mature ripe individuals and may be thought of as breeding aggregations resulting from the concentration of otherwise widespread individuals and smaller aggregations, in suitable breeding areas. During August, adults were seldom taken in seine hauls along the shore, apparently having moved to deeper water. Adults were taken at depths of 18.9 m in minnow traps and one adult was removed from the stomach of a lake trout taken near the bottom in 36.6 m of water.

The vertical distribution of ninespine sticklebacks is greater than that of any other characteristically small species of fish in Cold Lake. This species is known to occur at depths of 109 m in Lake Superior (Dryer, 1966) and to at least 30 m, usually within 30 cm of the bottom in Crooked Lake, Indiana (Nelson, 1968). Nelson found that this species was never taken in less than 5 m of water and rarely from water warmer than 14°C, although it was taken at extremes of 5° and 25°C. Fourteen °C waters are not present except at the surface of Cold Lake until after mid-July, after which adult ninespine sticklebacks are uncommon in shallow water. Aggregations of young of the year often accompanied by one or two adults were observed in 1-3 m of water in August. The specimen obtained from the lake trout taken at 36.6 m may constitute a valid depth record for ninespine sticklebacks in Cold Lake but may have been eaten by the predator in much shallower water.

## The Trout-perch

The trout-perch, in Cold Lake, is known on the basis of two specimens collected in September of 1952 (UAMZ 400). Miller (1956) did not include this in his species list from Cold Lake. From discussions with M. Paetz, who assisted in the 1952 collection, it appears that this species was, at best, locally abundant in atypical portions of the lake; the temporary tributary to English Bay and in the sheltered water near the town dock. No specimens were collected, or found in predator stomachs during the present study. Elsewhere trout-perch are important forage fish for walleye, pike, burbot and lake trout (Lawler, 1963; McPhail and Lindsey 1970; Scott and Crossman 1973).

## Slimy Sculpin

The slimy sculpin is the only cottid known to occur in Cold Lake (Paetz and Nelson, 1970). Miller (1956) reported "Rice's" sculpin, however all specimens examined from Cold Lake in the present study were slimy sculpins. This species was seen or collected in most areas around the lake shore (figure 15) and in the Medley River. It appeared to be most abundant in the riffles within the river, the river mouth and rocky margins along the lake shore. Specimens were occasionally seen or collected along sandy shorelines such as at North Bay where they were most frequently found under sunken logs. Specimens were also found in suitably sized cracks or holes in sunken logs that were entangled by gill-nets. Only two specimens were taken in minnow traps, and these were from areas where they were known to be abundant. Occasionally specimens were taken in small (3/4-1 1/2" stretched mesh) gill-nets. Slimy sculpins in Cold Lake occupy a depth range from 0.5m to at least 9 m, the maximum depth at which they were taken during the present study. In Lake Michigan this species is common from 5.5 - 82.3 m (Scott and Crossman, 1973), in Lake Superior it is most abundant from 91.4 - 107.9 m (Dryer, 1966) while in Great Bear and Keller Lakes (N.W.T.) they were found in shallow, rocky areas where they encounter current or wave action and were only found to a maximum depth of 10 m in the latter (McPhail and Lindsey, 1970).

The onset of spawning for this species is associated with temperatures of 5-10°C in New York (Scott and Crossman 1973) and occurred as early as May in Great Bear Lake (McPhail and Lindsey, 1970). Ripe females were found in mid-May at Cold Lake but the spawning period may be extended, as eggs, presumably of this species, were taken from lake whitefish as late as July.

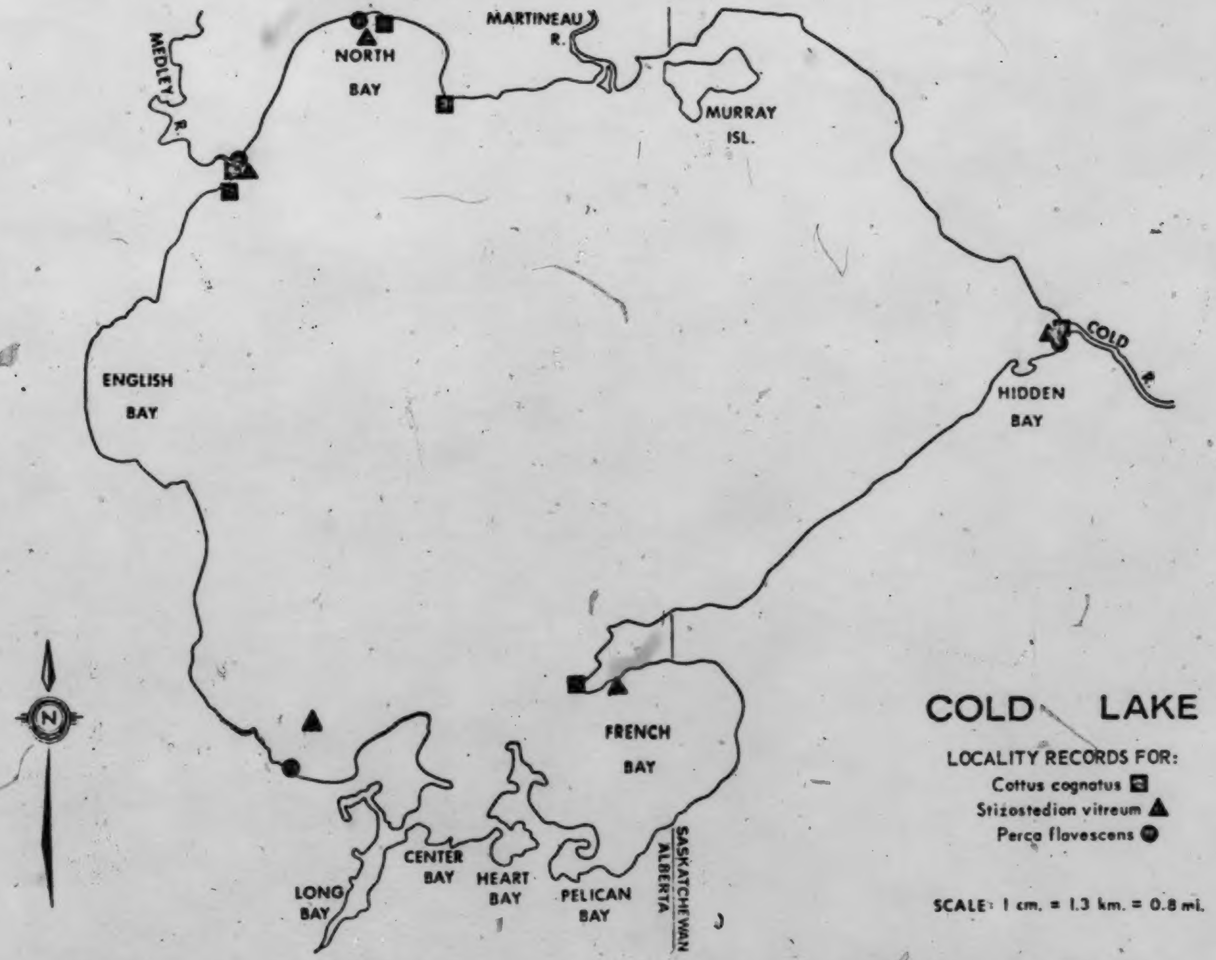

COLD LAKE
LOCALITY RECORDS FOR:
Cottus cognatus ■
Stizostedion vitreum ▲
Perca flavescens ●
SCALE: 1 cm. = 1.3 km. = 0.8 mi.
MEDLEY R.
NORTH BAY
MARTINEAU R.
MURRAY ISL.
COLD R.
HIDDEN BAY
ENGLISH BAY
FRENCH BAY
LONG BAY
CENTER BAY
HEART BAY
PELICAN BAY
SASKATCHEWAN
ALBERTA
N

FIGURE 14 Locality records for Cottus, Stizostedion and Perca

Early studies of the food of slimy sculpins were summarized by Koster (1937). Principal food items were aquatic invertebrates, crustaceans and small fish, with aquatic invertebrates accounting for over 50% of the diet. Stomachs examined from Cold Lake specimens contained amphipods exclusively or with a small amount of aquatic insect larvae. One large (80 mm) individual removed from a northern pike stomach had a smaller specimen partially within its mouth but it is difficult to attribute this to cannibalism with any certainty.

Slimy sculpins are preyed upon by a number of predaceous fishes including northern pike, lake trout and burbot (Scott and Crossman, 1973). In Cold Lake they are important in the diet of northern pike and have also been noted in walleye stomachs.

## The Distribution of Walleye

Adult walleye appear to be sparsely scattered throughout moderately deep water during the summer with the only notable concentrations being in and near the mouth of the Martineau River and the lake shore immediately in front of the Cold River (see figure 15). In 1971 and 1972 they were taken by anglers in French and Long Bays until July, after which time they were seldom taken, possibly due to vertical migration to deeper waters or migration to other areas in the lake. The Martineau River and the lake near its mouth are perhaps the only areas that are continually occupied by adults of this species throughout the open water season. Spawning occurs in shallow regions of Long and French Bays and in the Martineau River in late April and early May, at which time, concentrations of walleye are found in these areas. All adults sampled on and after May 10, 1972, were spent.

During 1971 and 1972 young of the year walleye were evident near the shore around much of the lake margin until August. As they grew larger they were found further from the shore and tended to become associated with the bottom rather than occupying all portions of the water column, especially the upper portion, as they did initially. Priegel (1963) found individuals 3.5 cm fork length or less near the surface of all areas of Lake Winnebago, Wisconsin, larger individuals occurring in deeper water. Age class $1^+$ walleye were occasionally encountered immediately off the Medley River mouth, in the mouth itself, and in a small stream tributary to English Bay, most specimens being taken near the bottom in gill-nets set in 2-3 m of water.

Schools of adult walleye are said to be "loose but discrete" (Scott and Crossman,1973). During the present study adult walleye were most frequently taken singly or in twos although one 100 yard set for one night yielded 23 specimens. They are the only large, characteristically piscivorous species in Cold Lake that occurs in schools. Young of the year walleye are not found in schools per se, but form part of a polytypic aggregation of small fishes including a few cyprinids, and young of the year lake whitefish, white and longnose suckers, and yellow perch, found along the lake margin until late summer.

## Predation by Walleye

No stomachs of adult walleye were collected during the present study but observations of the stomach contents of specimens taken near the Cold River in 1971 indicated that slimy sculpins and ciscoes were important food items. Cisco may be expected to be a dominant item in the diet of individuals occupying deep water during the summer. Two of eleven spent adults taken from a spawning area in mid-May contained amphipods, the remainder being empty. Forage fish did not appear to be abundant there at the time.

Young of the year walleye were observed to eat fish at sizes as small as 30 mm. Fifty specimens seined during late June of 1972 were examined and nearly all contained food in the form of small fish. Ten walleye from 30-39 mm fork length ($\bar{x}$ = 34.9) contained an average of 1.3 young of the year suckers approximately 18-20 mm long. Three of these walleye contained a small amount of aquatic insect remains in addition to the small suckers. Priegel (1963) found that walleye of less than 75 mm were predators of invertebrates, those of 10-50 mm preying upon _Leptodora_, _Diaptomus_, and chironomid larvae. At about 75 mm fish became the dominant food, white suckers being the most frequently eaten species. Young of the year suckers appeared to dominate the diet of young of the year walleye until late summer, by which time the walleye had attained sufficient size to prey upon other small fishes in Cold Lake.

## The Yellow Perch

Locality records for yellow perch are shown in figure 15. Throughout the study area of Cold Lake this species appeared to be represented largely, if not exclusively by age classes 0 and $1^+$. These young fish probably dispersed from more favorable habitat in the shallow weedy portions of French and Long Bays, the only areas in which adults are characteristically found. Yellow perch are usually found at temperatures of 19-20 C (Ferguson, 1958) and McPhail and Lindsey (1970) suggest that the northward extent of their range is limited by temperature. This species is considered to be a shallow water inhabitant and is not usually found at depths in excess of 9.2 m (Scott and Crossman, 1973). Owing to its great depth and cool water much of Cold Lake appears to be poor habitat for yellow perch. They form only a small portion of the aggregation of small fishes found along the lake margin but are more abundant near the Medley River mouth.

Invertebrates were the only food items found in the small (95 mm fork length) specimens examined.

The Iowa Darter

The Iowa darter was collected at only four locations during the present study (see figure 16), only one of which was part of the lake proper. The area bounded on the north and west by the town dock at Cold Lake is protected from a great deal of wave action and contains dense beds of rooted aquatic plants. Iowa darters inhabit clear, standing or slowly moving bodies of water, having rooted aquatic vegetation (Scott and Crossman, 1973) however collections from northwestern Canada have been from the shallows of clear sand or mud-bottomed lakes (McPhail and Lindsey, 1970). They were abundant at the sites associated with tributaries in Cold Lake during May and June, and frequently observed in the shallows. Specimens were difficult to collect by means of seining due to their small size, benthic habits and the unevenness of the substrate.

Iowa darters eat a broad range of benthic aquatic invertebrates (Keast, 1968). Keast found that the diversity and quantity of food taken by this species during the winter was greatly reduced and concluded that the quantity of food taken by Iowa darters during the winter was inadequate to maintain their body weight. The low inshore temperatures and their duration during the winter at Cold Lake result in it providing poor habitat for this species. Iowa darters

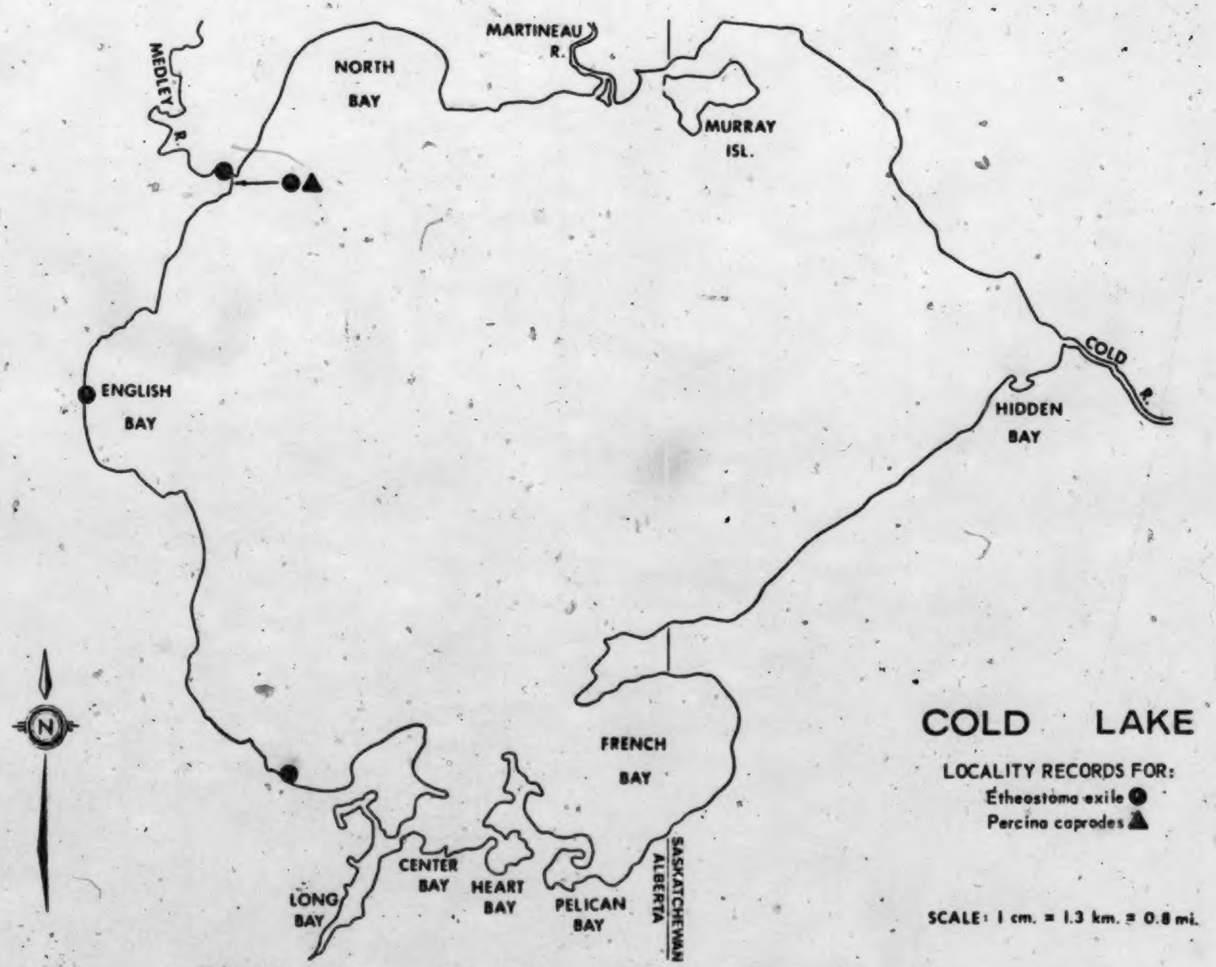

MEDLEY R.
NORTH BAY
MARTINEAU R.
MURRAY ISL.
ENGLISH BAY
COLD R.
HIDDEN BAY
N
FRENCH BAY
LONG BAY
CENTER BAY
HEART BAY
PELICAN BAY
SASKATCHEWAN
ALBERTA
COLD LAKE
LOCALITY RECORDS FOR:
Etheostoma exile ●
Percina caprodes ▲
SCALE: 1 cm. = 1.3 km. = 0.8 mi.

Figure 16 Locality records for Etheostoma and Percina

collected during this study were small, the maximum length noted being less than 40 mm. Adults in Canadian waters usually attain lengths of 51-58 mm (Scott and Crossman,1973) and the poor growth exhibited by this species in Cold Lake may be due to poor feeding during the long, cold winter.

The small size and benthic habits of this species minimize its potential as a piscivore, as fish small enough for it to prey upon are generally larvae swimming near the surface, or in mid-water. Iowa darters in aquaria were observed to eat young fish, including their own, but there appears to be no evidence for this in nature.

## The Logperch

A single specimen of the logperch was taken in a seine at the mouth of the Medley River in August of 1971. This is the first record of this species from Alberta (Roberts,1973), and Cold Lake is the western limit of the known range of this species. The same difficulties encountered when collecting Iowa darters may result in underestimating the abundance of this species. Logperch tend to occupy offshore waters in excess of 1 m and are thus often considered to be uncommon by collectors employing seines (Scott and Crossman,1973). This species has been taken at depths of up to 40 m (131') in Lake Erie (Trautman,1957).

Logperch feed on invertebrates, with midge and mayfly larvae and amphipods being important items (Dobie,1959;

Keast and Webb, 1966). Dobie also reports predation on a young of the year walleye by one of 116 logperch examined. Known predators of logperch include lake trout, northern pike and walleye, while white suckers and other logperch are known to eat their eggs (Scott and Crossman, 1973). Logperch were not identified from the stomachs of any piscivorous fishes during this study.

# FINAL DISCUSSION AND CONCLUSIONS

Northern pike appear to be the most abundant characteristically piscivorous fish in Cold Lake. They eat the greatest variety of forage fishes. They probably consume more fish per year than any other native fish, both as individuals and as a species, however their role as a piscivore is limited to relatively shallow water around the lake margin.

The lack of information concerning burbot and walleye in the shallows of Cold Lake reflects, in part, their scarcity in this region of the lake during the summer months. These species are probably most abundant in deep water during this time, and prey upon the abundant, ubiquitous cisco. The role of the burbot and walleye adults in the predator-prey relationships within the shallow, inshore regions during the summer is minor when compared to that of other species.

Adult yellow perch appear to be restricted to the weedy, shallow areas in French and Long Bays and are not important predators of fish throughout most of Cold Lake. While the young are distributed along the lake margin around much of the lake, they feed upon invertebrates and not other fishes.

While lake trout do not appear to be abundant in Cold Lake they are probably the major fish predator of the cisco. Lake trout appear to be the only characteristically piscivorous fish to occupy the pelagic region of the lake as do the cisco. As a result of reduction in the numbers of lake trout in Cold Lake due to the activities of man, predation upon cisco is probably greatly reduced from its former level. Coho salmon did not appear to utilize this species to the degree that was initially expected, and owing to the low temperatures encountered in the hypolimnion of Cold Lake would probably do so only in the upper portion of the waters occupied by cisco. The predator prey relationship between the lake trout and the cisco should be restored by the continuation of introductions of young lake trout, perhaps in greater numbers than at present. No other predator-prey combination occupies as much of the available habitat in Cold Lake as that of lake trout and cisco.

The lake whitefish and cisco are not characteristically piscivorous fishes but are sufficiently numerous and widespread within the lake to provide a significant source of predation on small fishes, even if only a small portion of their respective populations preys upon fish. During the period from late May to July lake whitefish eat large numbers of ninespine sticklebacks and their eggs, and perhaps those of other species.

Many of the potential forage species in Cold Lake are either uncommon or of restricted distribution and thus are not readily available to some, or all of the piscivorous species. Most of the cyprinids are restricted to tributaries or the lake margin near their mouths. The distribution of young of the year lake trout, burbot and all age classes of trout perch is uncertain. The young of the year lake trout may be expected to occupy deep water, as they have been noted to move rapidly into deep water, cooler than 10°C during the first year of their life (Rupp and Deroche, 1960). At this time they would be exposed to predation by adult lake trout, burbot, and perhaps walleye, although cannibalism among lake trout appears to be common only in the absence of other forage fish and does not always occur in these situations. Young burbot are not evident in shallow water as they are in other lakes, but may be present in water of moderate depth, especially in rock-bottomed areas such as those where burbot of age class $2^+$ are locally abundant. The status of the trout-perch in Cold Lake is uncertain.

The presumed distribution of the young of the year cisco appears to be unique in that, on the basis of negative evidence, it is within the limnetic region of the lake where there are few piscivorous fishes other than scattered lake trout. Predation by fishes on young cisco appears to be at a very low level and may result in high survival, overcrowding, and may be manifest in the stunted growth exhibited by cisco in Cold Lake. Young of the year lake whitefish are segregated from older age classes of whitefish during their first summer at least as they spend the first few months of their life close to the lake margin, perhaps as the result of temperature preference, and which also results in their segregation from predators.

The early hatching time of lake whitefish results in their outgrowing the first piscivorous fish with which they are associated, the young of the year of yellow perch and walleye. Soon after hatching in May shortly after the ice recedes from the shore, they are the most abundant species in a narrow (1 m) band along sandy shores, such as that along North Bay. Occasional ninespine sticklebacks, and rarely, slimy sculpins or cyprinids may be found here also. Ninespine sticklebacks and slimy sculpins were found to prey upon young of the year lake whitefish in aquaria, but there is no evidence that they do so along the margin of Cold Lake. In mid to late June this aggregation is enlarged by the addition of young of the year walleye, and in late June by young of the year suckers, both presumably having hatched in the Martineau and Medley Rivers. Lake whitefish are larger than the walleye at this time. Walleye as small as 30 mm begin to prey upon the sucker larvae in the aggregation. This aggregation persists along the shore until late July, the young walleye continuing to prey upon the young suckers. Predation upon suckers by walleye during the first year of their lives is likely a major factor in the early mortality of suckers in Cold Lake. There appears to be much less predation upon the older age classes of suckers by piscivorous fishes here. All of the fishes in this aggregation appear to be segregated from other piscivorous fishes until late in their first summer, by which time they have moved into water one or more m deep further from shore.

Ninespine sticklebacks are eaten by lake whitefish, cisco, lake trout, rainbow trout, coho salmon, northern pike, burbot, and probably walleye and yellow perch. They appear to be the chief forage fish in the diets of all the piscivorous fishes in the shallow portions of the lake at least. Ripe female ninespine sticklebacks are found in greater numbers than males in the stomachs of piscivorous fishes in Cold Lake and outnumbered males in northern pike stomachs by greater than three to one. In lake trout this ratio was in excess of fourteen to one. Females may be preyed upon selectively because they are larger than males and perhaps within this prey species only the largest specimens approach the optimum prey size for these large predators. Alternatively, the large, egg-laden females are likely more conspicuous and less capable of fleeing the predators than are the males or non-spawning individuals. It appears that the native piscivores prey almost exclusively upon adults. In the absence of other sources of predation, or mortality of young ninespine sticklebacks, it would appear that survivorship in young age classes is high while that of older age classes is reduced, which is most unusual. The life history of this important forage fish in Cold Lake requires further study to understand how, in the face of excessive predation upon the breeding females, this species is able to maintain itself in relatively high numbers, and to determine the true nature of survivorship in each age group.

Coho salmon were unique among the piscivorous fishes of Cold Lake for a number of reasons. No other large fish, including the coregonids, appeared to utilize aerial food or surface drift to the extent that coho salmon did. While cisco, and less frequently, lake whitefish, were observed to take food from the surface, none were encountered with more than the occasional invertebrate so derived in their stomachs, and this may be considered only a minor portion of their diets. Aerial food was not encountered in the stomach of any characteristically piscivorous fishes. In this regard coho salmon utilized a source of food virtually untapped by the native fishes. By preying upon adult caddis flies, it might be said that coho salmon compete indirectly with species that prey on the larvae of caddis flies such as the lake whitefish. It seems unlikely that the depredations of coho salmon upon adult caddis flies would cause any measurable reduction in the recruitment of these insects. Coho salmon also eat allochthonous material in the form of terrestrial invertebrates especially during their first and second years, which results in a decrease in the amount of autochthonous material consumed.

Coho salmon ate more juvenile lake whitefish than the combined total of all other piscivorous fishes examined during this study. The shallow water distribution of coho salmon and their ability to prey successfully upon schooling fishes, such as the young lake whitefish, results in predation upon the latter species by coho salmon as the young whitefish move further from the shore during the last half of their first summer of life. The presence of large numbers of coho salmon might have a detrimental effect upon the recruitment of this commercially valuable species, as they represent a source of predation unmatched by the native piscivorous fishes.

The inclusion of large numbers of young of the year ninespine sticklebacks is also unusual in the diet of native piscivorous fishes. Ninespine sticklebacks are preyed upon extensively by the native piscivorous fishes but it is generally the larger individuals that are taken. This may be the result of size selective predation, larger predators such as lake trout and northern pike being morphologically equipped to handle prey items more efficiently if they are above a certain (undetermined) size, and/or tending to prey on those items that give them the greatest return relative to the energy expended in feeding. The swimming ability of ripe, swollen female ninespine sticklebacks is likely reduced, thus making them an attractive target for predators. Coho salmon appear to include fish in their diet as soon as they are large enough to capture and swallow them successfully. Coho salmon begin to include adults in their diet shortly before the young of the year are available, and perhaps the salmon too, prey selectively on large young of the year individuals as newly hatched individuals were not encountered in salmon stomachs. Coho salmon appear to gorge themselves by repeatedly attacking aggregations of young of the year ninespine sticklebacks. The low rate of predation upon young of the year ninespine sticklebacks by the native piscivorous fishes may result in more young surviving to adulthood at which time they are preyed upon by lake trout, northern pike, burbot and occasionally coregonids. The numbers of ninespine sticklebacks eaten by individual coho salmon is probably far greater than those for lake trout and northern pike in spite of the greater average size of the latter species. While lake trout appear to prey exclusively upon ninespine sticklebacks during the period May-July and are found to contain large numbers of them, the more numerous northern pike, although less selective in their feeding, consume more ninespine sticklebacks and may be considered the major predator of this species among the native piscivorous fishes of Cold Lake.

Northern pike appear to be conservative predators in Cold Lake, eating sufficient food to maintain themselves, grow slowly, mature and spawn. While their growth, with respect to length attained, approximates or may even exceed that of coho salmon of the same age during the first year of their lives, it is relatively slower during the second and succeeding years. There appears to be a marked contrast between the life history strategies of coho salmon and northern pike. Coho salmon and the other species of Onchorhynchus feed voraciously and grow rapidly during the saltwater phase of their lives. This may be of advantage in that larger females can produce more and/or larger eggs, and are less restricted in the size of substrate material they are able to utilize when digging their redds. Large individuals of both sexes are better equipped for stemming currents and negotiating rapids in a shorter period of time than are smaller, otherwise similar fishes and also have greater energy reserves for sustaining migration. Living within a single body of water throughout their lives, northern pike need not make lengthy migrations, stem strong currents, and store energy for migrations such as those undertaken by salmon. Large size is also adaptive for northern pike for feeding and reproduction however. Larger predators are generally able to handle larger prey and this may result in a greater return to the predator than expending a greater amount of energy to capture an equivalent amount of nutrients from a large number of small prey items. The importance of large size may be reflected in the sexual dimorphism exhibited in the growth of northern pike adults, females being larger than males, and as with other species, able to lay more and/or larger eggs than if the females were small. Rapid growth however does not appear to be of great advantage and may be a disadvantage in that it would require a higher rate of predation and possibly a reduction in the prey population available to the predator. In the confines of a relatively small body of water such a strategy may be regarded as imprudent. Most fresh water piscivorous fishes appear to have a life history and growth strategy similar to that of the northern pike in that growth is relatively slow and adults may spawn a number of times. That of the Pacific salmons may be regarded as a specialization that is made possible by, and at a selective advantage for, their anadromous way of life.

It appears that over winter survival of coho salmon was poor, perhaps as a result of their activity being limited by the unusually cold (for Pacific salmon) water temperatures. Reduced swimming speed would render them less effective as piscivores and at the same time they would more readily fall prey to native fishes, notably the northern pike. The size and condition of coho salmon caught early in the open water season reflects poor feeding during the winter and there is little or no growth during the period from November to June.

By feeding voraciously upon the abundant aerial food and ninespine sticklebacks coho salmon grew rapidly during the period from June to August or early September. The precocious maturation of some male salmon from each introduction may also be indicative of favorable feeding and growing conditions.

Due to the differential handling of each introduction, it is difficult to attribute any differences in feeding, growth, behavior and survival of each to racial differences between the stocks of salmon introduced.

# SUMMARY

1. The piscivorous fishes of Cold Lake all prey upon ninespine sticklebacks.
2. Ninespine sticklebacks are the principal food of northern pike throughout the year and of lake trout during early summer.
3. Northern pike and lake trout are the principal predators of ninespine sticklebacks among the native piscivorous fishes of Cold Lake.
4. During early summer some lake whitefish eat ninespine sticklebacks.
5. The native piscivorous fishes prey upon adult ninespine sticklebacks and rarely utilize the young of the year of this forage species.
6. Ninespine sticklebacks are the forage fish most utilized by introduced coho salmon in terms of numbers, volume and frequency of occurrence in stomachs containing food.
7. Coho salmon eat all age classes of ninespine sticklebacks and were the only piscivorous fish found to prey upon young of the year lake whitefish.
8. Introduced coho salmon were able to utilize the abundant forage fishes as well as invertebrates and grew rapidly during the summer months (see figure 17).

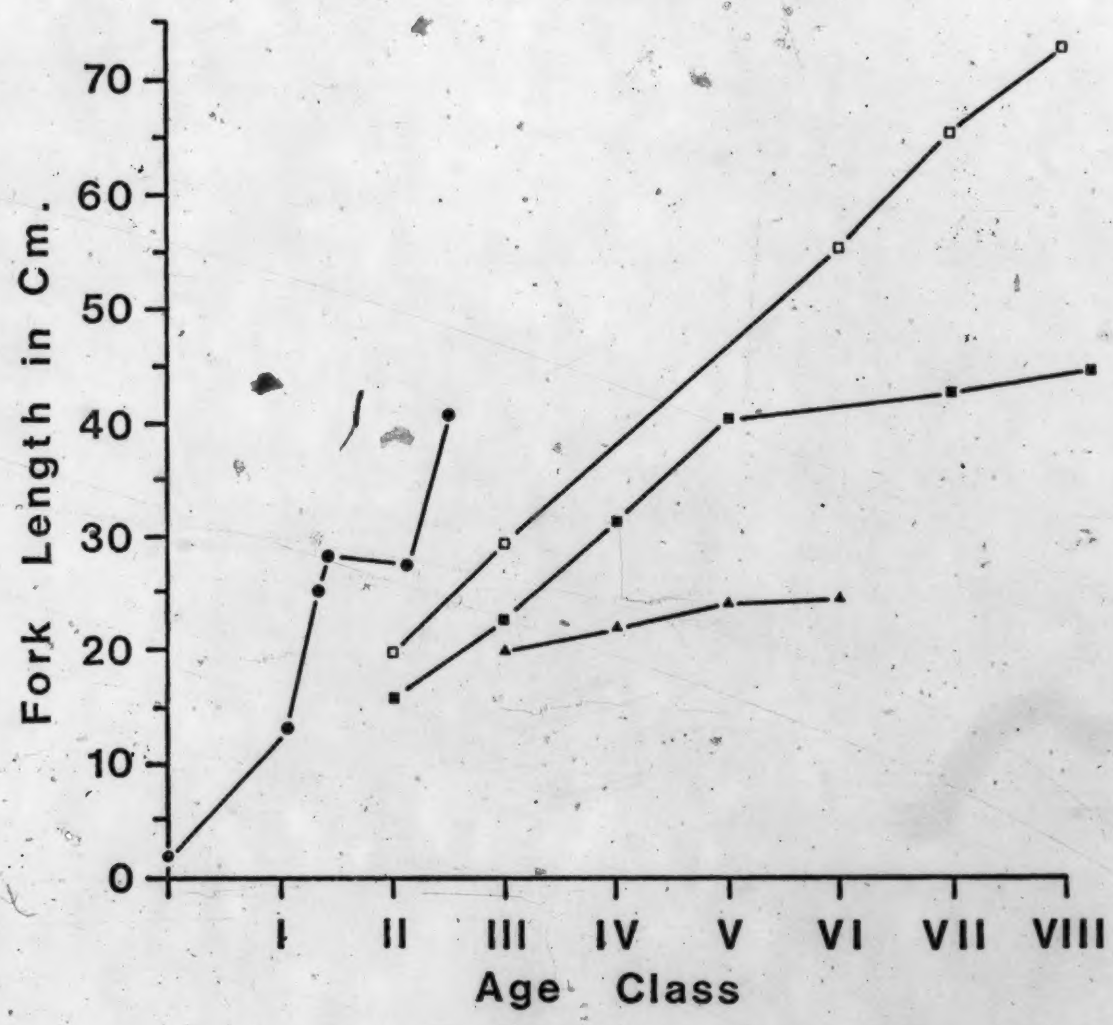


Figure 17. The relative growth of four species of fish in Cold Lake. ● coho salmon; □ northern pike; ■ lake whitefish; ▲ cisco. (After Paetz and Zelt, 1974, and R. Leong, unpublished data).

9. Spatial overlap of fish species in shallow water permitting predator prey relationships during May, June, July, August and September may be summarized as follows:

| Predator | May | June | July | August | September |
|---|---|---|---|---|---|
| | | | Prey | | |
| Coho salmon | ? | P | P | P,Lw(y-o-y) | P,Lw,C |
| Northern pike | P | P,C,Co | P,C,Co | P,Co | P,Co |
| Lake trout | P ? | P | P | C | C |
| Burbot | ? | P | P | P | P |
| Walleye (y-o-y) | - | - Cat | Cat | Cat | ? |

Cat = *Catostomus*

C = Cisco

Co = *Cottus*

Lw = Lake whitefish

P = *Pungitius*

y-o-y = young of the year

Only those prey species occurring in at least 5% of the stomachs containing food are included.

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# APPENDIX I

## SUBMERGENT AND EMERGENT ROOTED AQUATIC PLANT SPECIES FOUND AT COLD LAKE, ALBERTA[a]

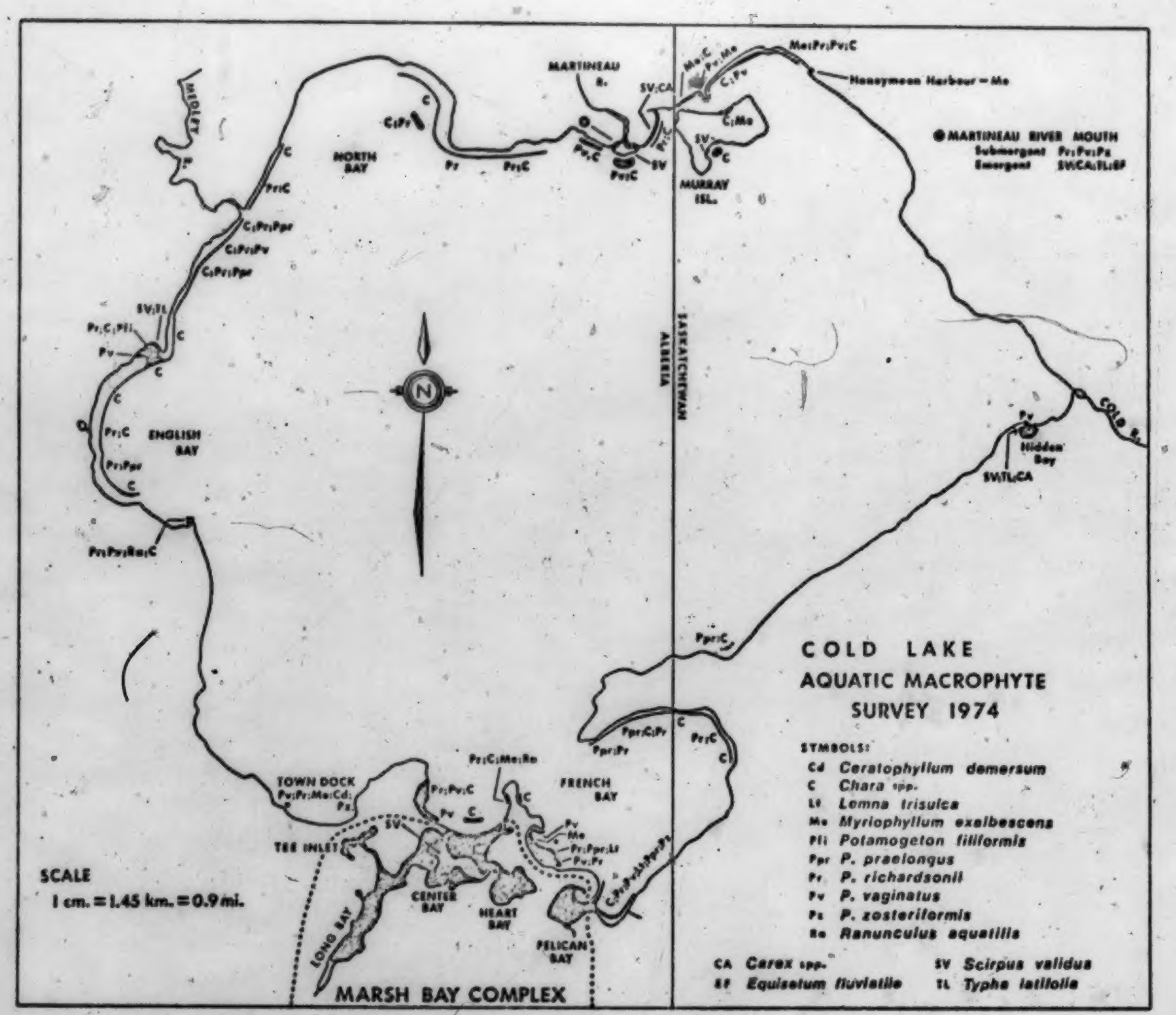
Submergent

- *Potamogeton vaginatus*
- *P. richardsoni*
- *P. praelongus*
- *Chara* sp.
- *Myriophyllum exalbescens*
- *Ranunculus aquatilis*
- *Fontinalis* sp.
- *Eleocharis acicularis*
- *P. Filiformis*
- *Ceratophyllum demersum*
- *P. pectinatus*
- *P. gramineus*
- *Sparganium fluctuans*
- *Callitriche hermaphroditica*
- *Elodea canadensis*

Emergent

- *Scirpus validus*
- *Typha latifolia*
- *Carex* spp.
- *Equisetum fluviatilis*

[a] Gallup, D. N., Dept. of Zool., U. of A. Unpublished data "A Survey of Alberta Lakes". Identified by J. Weisgerber.


COLD LAKE
AQUATIC MACROPHYTE
SURVEY 1974
SYMBOLS:
Cd Ceratophyllum demersum
C Chara spp.
Lt Lemna trisulca
Me Myriophyllum exalbescens
Pfi Potamogeton filiformis
Ppr P. praelongus
Pr P. richardsonii
Pv P. vaginatus
Pz P. zosteriformis
Ra Ranunculus aquatilis
CA Carex spp.
EF Equisetum fluviatile
SV Scirpus validus
TL Typha latifolia
MARTINEAU RIVER MOUTH
Submergent Pr;Pv;Pz
Emergent SV;CA;TL;EF
SCALE
1 cm. = 1.45 km. = 0.9 mi.
SASKATCHEWAN
ALBERTA
N
MEDLEY R.
MARTINEAU R.
NORTH BAY
ENGLISH BAY
MURRAY ISL.
Honeymoon Harbour – Me
Hidden Bay
COLD R.
TOWN DOCK
Pv;Pr;Me;Cd;Pz
FRENCH BAY
TEE INLET
LONG BAY
CENTER BAY
HEART BAY
PELICAN BAY
MARSH BAY COMPLEX
Me;Pr;Pv;C
Me;C
Pv;Me
C;Pv
C;Me
SV;CA
SV
Pv;C
Pr;C
Pr
C;Pr
C
C;Pr;Ppr
C;Pr;Pv
SV;TL
Pr;C;Pfi
Pr;Ppr
Pr;Pv;Ra;C
Ppr;C
Ppr;C;Pr
Ppr;Pr
SV;TL;CA
Pr;C;Me;Ra
Pr;Pv;C
Pr;Ppr;Lt
Pv;Pr

# APPENDIX II

## PISCIVOROUS WATERFOWL OBSERVED AT COLD LAKE

Common loon (*Gavia immer*)

Red-necked grebe (*Podiceps grisegena*)

Horned grebe (*P. auritus*)

Eared grebe (*P. caspicus*)

Western grebe (*Aechmophorus occidentalis*)

Pied-billed grebe (*Podilymbus podiceps*)

White pelican (*Pelecanus erythrorhynchus*)

Double-crested cormorant (*Phalacrocorax auritus*)

Great blue heron (*Ardea herodias*)

American bittern (*Botaurus lentiginosus*)

Common merganser (*Mergus merganser*)

Red-breasted merganser (*Mergus serrator*)

Bald eagle (*Haliaeetus leucocephalus*)

Osprey (*Pandion haliaetus*)

Herring gull (*Larus argentatus*)

California gull (*L. californicus*)

Ring-billed gull (*L. delawarensis*)

Common tern (*Sterna hirundo*)

Belted kingfisher (*Megaceryle alcyon*)